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The Systematics of the Frogs of the
Hyla rubra Group in Middle America

BY

JUAN R. LEÓN

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INTRODUCTION

The tree frogs of the *Hyla rubra* group are abundant and form a conspicuous element of the Neotropical frog fauna. Representatives of the group occur from lowland México to Argentina; the greatest diversity is reached in the lowlands of southeastern Brazil (Cochran, 1955). The group apparently originated in South America; the endemic Central American species evolved from stocks that invaded Middle America after the closure of the Colombian Portal in the late Pliocene.

Dunn (1933) partially defined the *rubra* group as it occurs in Central America. Cope (1865, 1876, 1887), Brocchi (1881), Boulenger (1882), Günther (1901), Noble (1918), Kellogg (1932), Dunn and Emlen (1932), Stuart (1935), and Gaige (1936) dealt with the Middle American species now considered to make up the *rubra* group. More recently, Taylor (1952, 1958), Fouquette (1958), Starrett (1960), and Duellman (1960, 1963, 1966a) studied aspects of the taxonomy and biology of the species of this group. The five species of the *rubra* group in Central America have received ten different names. One species, *Hyla staufferi*, has received five names (two subspecies are recognized herein). *Hyla boulengeri* was named in the genus *Scytotis*, but the type species of *Scytotis* is a member of the genus *Phrynohyas* Fitzinger, 1843 (Duellman, 1956.)

Little has been published concerning the ecology, life history, osteology, and mating calls of the Middle American species of this group. The purpose of the present report is to describe the species occurring in Middle America and to comment on their distributions, ecology, cranial osteology, and mating calls, and in so doing provide evidence for the evolutionary history of the species inhabiting Middle America.

Acknowledgments

For permission to examine specimens in their care, I am grateful to Drs. Richard G. Zweifel, American Museum of Natural History (AMNH); Robert F. Inger, Field Museum of Natural History (FMNH); Ernest E. Williams, Museum of Comparative Zoology (MCZ); Hobart M. Smith, University of Illinois Museum of Natural History (UIMNH); Charles F. Walker, University of Michigan Museum of Zoology (UMMZ); Jay M. Savage, University of Southern California (USC); James A. Peters, United States National Museum (USNM); Richard J. Baldauf, Texas Cooperative Wildlife Collection (TCWC); and W. Frank Blair, Texas Natural History Collection (TNHC). KU refers to specimens in the Museum of Natural History, University of Kansas. For the loan of tape-recordings of mating calls I thank Drs. W. Frank Blair, University of Texas, and Richard G. Zweifel, American Museum of Natural History.

I am indebted to the Ford Foundation-Universidad de Oriente (Venezuela) Science Project for a scholarship which enabled me to study for two years at The University of Kansas, foster institution of the project. I have benefited by being able to work in the Museum of Natural History at The University of Kansas and I am grateful to Dr. E. Raymond Hall, Director, for providing space and equipment.

I gratefully acknowledge the assistance and advice of Dr. William E. Duellman, who suggested and directed this work, made available specimens under his care and gave much of his time in reading the manuscript and suggesting improvements. I am grateful to Dr. Frank B. Cross who critically read the manuscript and made many editorial suggestions. I am indebted to Linda Trueb for assistance with the osteological aspects of this study; she helped to clarify many confusing points. I am grateful to Charles W. Myers for making available his field notes on these frogs in Panamá, to Arthur C. Echternacht for reading part of the manuscript, and to John D. Lynch for many suggestions and helpful criticisms. The illustrations were executed by David M. Dennis.

Materials and Methods

For the purposes of the present study I examined 1383 preserved specimens, 50 skeletons, and 9 lots of tadpoles. External characteristics used in the analysis of variation are those currently employed in the study of anuran systematics. Twelve measurements and six proportions were taken in the manner described by Duellman (1956). Only the most important references are given in the synonymies, except those of the two subspecies of *Hyla stauferi*, which are more nearly complete. The taxonomic history of each frog is discussed under *Remarks* in each account. The cranial osteology was studied by using skeletons and cleared and stained specimens of all species. Developmental stages of tadpoles were determined from Gosner's (1960) table. Personal field work in Central America in the summer of 1966 provided an opportunity to make observations on the ecology, calling sites, and color in life; these data were supplemented by field notes from, and discussions with, Dr. William E. Duellman and Charles W. Myers.

The mating calls of the frogs were recorded in the field on Magnemite and Uher Tape Recorders by Dr. Duellman in the course of his work on the hylid frogs of Middle America—supported by grants from the National Science Foundation (G-9827 and GB-1441). These recordings, plus those borrowed from other institutions, provided 50 tapes for analysis of the mating calls. The calls were analyzed on a Vibralyzer (Kay Electric Company).

THE HYLA RUBRA GROUP

Definition.—The species forming the group are small to moderate-sized tree frogs (maximum snout-vent length of males of various species 20-49 mm.), distinguished from other groups in the genus *Hyla* as follows: Brown, grayish brown, or yellowish tan above; thighs plain, marbled with dark brown, or having vertical bands; vocal sac single, median, subgular; snout flat, protruding, rounded or pointed; webbing between fingers reduced or absent; web between first and second toes reduced to fringe on second toe, rest

of toes about half webbed; tarsal fold reduced or absent; shanks robust; inner metatarsal tubercle larger than outer; prevomerine teeth on transverse ridges between small to large sized choanae; skull generally longer than wide; nasals large (length more than 40 per cent total length of skull) and having pointed maxillary processes; maxillary bearing small ventromedial palatine process; quadratojugal slender, always joined to maxillary by bony suture; auditory region of proötic slender and short; delicate spatulate columella ventral to crista parotica, broad basally, compressed anterolaterally, slightly rounded distally; anterior arm of squamosal extending about half distance to maxillary; sphenethmoid wider than long; frontoparietal fontanelle present or absent; prevomerine, premaxillary, and maxillary teeth present; prevomer with two lateral processes forming incomplete bony margin to internal nares; tadpoles having pointed xiphicercal tail, snout short, rounded; 2/3 tooth rows; dorsal fin deeper than ventral fin; sinistral spiracle; short dextral anal tube not reaching edge of ventral fin; mating calls consisting of single long note or series of short notes.

Composition.—This group contains about 24 currently recognized species, most of which occur in Brazil. Only five species—*boulengeri*, *elaeochroa*, *foliamorta*, *rubra*, and *staufferi* with two subspecies—occur in Central America. *Hyla boulengeri* and *rubra* are widespread in South America, and *foliamorta* occurs in Colombia, whereas the other species are known only from Middle America.

Distribution.—The species of the *Hyla rubra* group range from the lowlands of northern Argentina and Bolivia to southern Tamaulipas and Guerrero, México.

Comments.—In Central America two subgroups of species can be recognized. *Hyla boulengeri* and *H. foliamorta* are distinctive in the large size of adults (snout-vent lengths 41-49 mm.); both have prominent bars on the thighs, a well-defined interorbital triangular mark, blotches or spots dorsally, and large choanae. *Hyla elaeochroa*, *H. rubra*, and *H. staufferi* are smaller (snout-vent lengths 29-40 mm.); they have the thighs weakly barred or vermiculate anteriorly and posteriorly or unmarked, an ill-defined interorbital triangular mark, linear markings dorsally, and small choanae.

Key to Species and Subspecies

- | | |
|---|---|
| 1. Larger frogs (males to 49 mm. snout-vent length); thighs strongly barred; supratympanic fold black; dorsum blotched or spotted | 2 |
| Smaller frogs (males to 40 mm. snout-vent length); thighs weakly barred or plain; supratympanic fold pale brown; dorsum usually having linear pattern | 3 |

2. Dorsum tuberculate; snout subacuminate; vocal sac flecked with brown; tarsal fold rudimentary; web absent between fingers; black spots absent in scapular region *H. Boulengeri*
Dorsum smooth; snout pointed; vocal sac dark gray; tarsal fold absent; trace of web between fingers; two or more elongate dark spots in scapular region *H. foliamorta*
3. Snout-vent length more than 30 mm.; tympanum $\frac{3}{4}$ to $\frac{1}{2}$ diameter of eye; prevomerine elevations about size of choanae 4
Snout-vent length less than 30 mm.; tympanum less than $\frac{1}{2}$ diameter of eye; prevomerine elevations smaller than choanae 5
4. Thighs mottled posteriorly; discs on fingers about $\frac{1}{2}$ size of tympanum; faint dark line from nostril to eye *H. rubra*
Thighs faintly barred or plain posteriorly; discs on fingers about size of tympanum; distinct dark line from nostril to eye *H. elaeochroa*
5. Dorsum brown with irregular dorsolateral stripes and interrupted paravertebral stripes; two transverse bars on shanks; interorbital bar present *H. stauferi stauferi*
Dorsum gray with complete dorsolateral and paravertebral stripes; longitudinal stripe on shank; interorbital bar absent *H. stauferi altae*

Key to Known Tadpoles

1. Entire lower beak black; beaks moderate-sized, serrate; dorsal fin high, extending to middle of back 2
No more than half of lower beak black; beaks small, finely serrate; dorsal fin lower, barely extending onto body 3
2. Papillae present only laterally *H. Boulengeri*
Papillae present laterally and ventrally *H. foliamorta*
3. Distinct brown stripe from nostril to eye; two stripes below eye, *H. elaeochroa*
Faint stripe from nostril to eye; no stripe below eye *H. stauferi*

ACCOUNTS OF SPECIES AND SUBSPECIES

Hyla Boulengeri (Cope)

Scytotis Boulengeri Cope, Bull. U. S. Natl. Mus., 32:12, December 1, 1887 [Holotype.—USNM 13974, from "Nicaragua"; J. A. McNiel, collector].

Hyla Boulengeri: Günther, Biologia Centrali-Americana, Reptilia and Batrachia, p. 267, June 1901. Noble, Bull. Amer. Mus. Nat. Hist., 38:339, June 1918. Taylor, Univ. Kansas Sci. Bull., 35:856, July 1, 1952.

Diagnosis.—Size large (δ to 49 mm., η to 53 mm.); skull as long as wide; frontoparietal fontanelle present; snout subacuminate; canthus not pronounced; choanae large; tongue cordiform, slightly longer than broad; interorbital triangle tubercular; skin on dorsum tuberculate; tarsal fold reduced or absent; thighs, shanks, and tarsi boldly barred with dark brown and pale yellow-green in life.

Description.—Head flattened, longer than wide; snout projecting beyond lower lip; loreal region oblique; canthus not pronounced; length of eye less than interorbital distance; tympanum large, about 70 per cent of diameter of eye; interorbital triangle distinct; arms short; fingers lacking web; palmar tubercle tripartite; subarticular tubercles distinct; long tubercle on base of first finger; discs truncate; legs long; tarsal fold reduced or absent; inner metatarsal

tubercle rounded, larger than outer, both elevated; subarticular tubercles distinct; one phalanx free of web on second, third, and fifth toes, three free on fourth toe (Fig. 1A and B); skin tuberculate on dorsum, less so on flanks; skin of belly granular, that on chest and throat weakly granular; tongue cordiform, longer than wide, free and notched behind; vocal slits large, lateral to tongue.

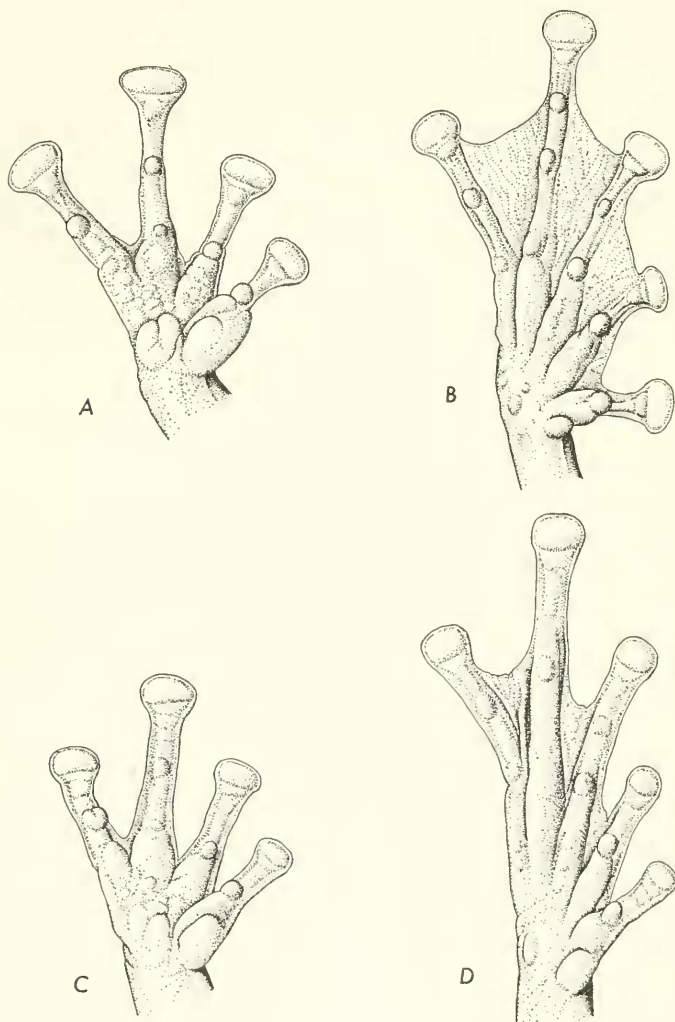


Fig. 1. A and B.—Hand and foot of *Hyla boulengeri* (KU 102173), $\times 3$. C and D.—Hand and foot of *Hyla s. staufferi* (KU 57790), $\times 6$

In life, dorsum tan or brown with dark spots on snout, head, and scapular region; interorbital triangle and blotch posteriorly on dorsum dark brown;

flanks pale green; groin pale green or orange, mottled with dark brown; thighs tan or brown above with dark transverse bars on anterior and posterior surfaces; spaces between bars green or orange; inner surfaces of shanks and outer surfaces of tarsi brown and orange; foot brown above; forelimbs brown and pale green above, weakly barred; belly creamy white with scattered brown spots; vocal sac creamy white flecked with brown; lower jaw brown with white spots on lips (Pl. 1A).

In preservative, head and dorsum dark brown with triangular spot between eyes; dark spots on head and scapular region and dark brown blotch posteriorly on dorsum; flanks creamy white with brown spots; groin creamy white mottled with dark brown; thighs brown above with dark brown transverse bars on anterior and posterior surfaces; inner surfaces of shanks and outer surfaces of tarsi barred with pale brown; dorsal surface of foot mottled brown and creamy white; ventral surface of foot and toes pale brown; forelimbs faintly barred with pale brown; belly white with a few pale brown spots; vocal sac flecked with pale brown; lower jaw marked with small white spots on lips.

Variation.—Geographic variation is evident in the snout-vent length, tibia length, and foot length, all in relation to snout-vent length, and the relative size of the tympanum to the eye (Table 1). The largest specimens are from the humid Pacific lowlands of Costa Rica; individuals from the Caribbean lowlands of Costa Rica, Canal Zone, and South America are smaller. A general trend for increase in size extends from South America to the Pacific lowlands of Costa Rica.

Most variation in color does not seem to be correlated with geography; color variation is nearly as great within a given population as between separated populations. However, most specimens from Rincón de Osa, Puntarenas Province, Costa Rica, are dusky brown, but a few are darker. In comparison with specimens from the Caribbean lowlands of Central America, specimens from the Pacific slopes in Costa Rica have a darker interorbital triangle. In some specimens from the latter area rugosities are present on the borders of the interorbital triangle, on the snout, on the upper eyelid, and on the heel. Specimens from the Caribbean lowlands are less tuberculate, and most individuals from there lack rugosities on the tarsus. Living individuals from Puerto Viejo, Heredia Province, Costa Rica, and from the Canal Zone, Panamá, are brown above with a metallic green tint. Rugosities are present on the posterior edges of the forelimbs in some specimens from throughout the range. In most respects, specimens from the Canal Zone resemble those from the Caribbean lowlands of Costa Rica more than they resemble those from the Pacific lowlands of Costa Rica, but some individuals from the Canal Zone are less metallic above and have small white spots dorsally on the body, head, and limbs.

A moderate amount of color change from night to day has been noted. At night, a male from Puerto Viejo, Heredia Province, Costa Rica, was grayish tan above with slightly darker markings; the flanks were pale yellowish green. By day, the dorsum was brown with darker markings, and the throat was pale gray with white flecks; the rest of the venter was creamy white. The groin was pale green with black mottling; the anterior and posterior surfaces of the thighs and inner edges of the tarsi were greenish yellow with black bars.

TABLE 1.—Geographic Variation in Size and Proportions in Males of *Hyla boulengeri*.
(Means in parentheses below observed ranges.)

Locality	N	Snout-vent length (mm.)	Tibia length/ snout-vent	Tympanum/ eye	Foot length/ snout-vent
Costa Rica: Tilarán.....	23	37.4-48.7 (43.8)	0.52-0.58 (0.55)	0.62-0.76 (0.71)	0.39-0.45 (0.42)
Costa Rica: Rincón de Osa.....	10	41.4-46.1 (44.0)	0.54-0.60 (0.57)	0.63-0.80 (0.74)	0.40-0.45 (0.43)
Costa Rica: Alajuela Province...	13	35.6-43.1 (39.8)	0.55-0.60 (0.57)	0.63-p.78 (0.69)	0.41-0.46 (0.44)
Costa Rica: Puerto Viejo.....	25	37.5-42.9 (41.6)	0.51-0.62 (0.55)	0.63-0.79 (0.71)	0.38-0.46 (0.43)
Costa Rica: Suretka.....	9	38.7-42.0 (41.0)	0.56-0.58 (0.56)	0.53-0.72 (0.62)	0.35-0.45 (0.42)
Panamá: Canal Zone.....	16	36.7-42.9 (39.0)	0.52-0.58 (0.54)	0.70-0.78 (0.74)	0.40-0.44 (0.42)
Venezuela: Santomé.....	4	35.5-40.9 (38.5)	0.45-0.48 (0.46)	0.63-0.67 (0.65)	0.36-0.40 (0.38)

TABLE 2.—Comparison of Mating Calls in the *Hyla rubra* Group.
(Means in parentheses below observed ranges.)

Species	N	Notes per call group	Duration of note (sec.)	Pulses per second	Fundamental frequency (cps)	Major frequencies (cps)	
						Lower	Upper
<i>H. boulengeri</i>	8	1	0.24-0.47 (0.35)	80-120 (101)	70-74 (71)	1400-1820 (1611)	2520-3182 (2840)
<i>H. foliamorla</i>	7	1	0.23-1.86 (0.69)	50-60 (51)	52-61 (56)	912-1026 (918)	2736-3477 (3055)
<i>H. elaeochroa</i>	15	2-95 (19)	0.12-0.24 (0.17)	40-50 (42)	48-65 (57)	1254-1586 (1499)	2562-3477 (2911)
<i>H. s. staufferi</i>	18	2-77 (23)	0.13-0.23 (0.18)	100-130 (120)	96-130 (106)	1582-1872 (1743)	1962-3744 (3056)
<i>H. s. altae</i>	7	2-22 (11)	0.14-0.18 (0.15)	110-130 (120)	104-117 (112)	1853-2106 (2008)	3379-4056 (3775)

Cranial Osteology.—The skull of *Hyla boulengeri* is as long as it is wide, and is flat; the premaxillary is small and bears 13 to 17 teeth (mean for 6 specimens, 14.9). The alary processes of the premaxillaries are widely separated, concave posteriorly, and vertical. Ventrally, the premaxillary is connected to the prevomer by bony tissues. The maxillary is slender and bears 70 to 91 teeth (mean for 6 specimens 78.1). The pars facialis of the maxillary is laterally convex and about four times as high as the pars dentalis.

The nasal is large (its length about 40 per cent of total length of skull), and pointed anteriorly and posteriorly in dorsal view. The nasals are separated anteromedially by the cartilaginous septum nasi. One or two protuberances are present on the midlateral concavity of the nasal. Posteriorly, the nasal overlaps the sphenethmoid and articulates with the palatine. Dorsally the sphenethmoid is large, pentagonal, and completely ossified. The frontoparietal is elongate, smooth, and bears a small supraorbital process on the anterior edge of the orbit. A keyhole-shaped frontoparietal fontanelle is present; the fontanelle is narrow anteriorly and wide posteriorly.

The bony part of the proötic is separated dorsally from the squamosal by the cartilaginous crista parotica. The squamosal is small, its anterior arm slender and pointed. The posterior arm of the squamosal is pointed terminally and articulates with the proötic medially.

The prevomer is large and elongate. Anteriorly the prevomer is connected to the maxillary-premaxillary articulation; posteriorly, the prevomer is separated from the sphenethmoid by cartilage. Each prevomer bears six to nine teeth. The palatine is present and edentate. The anterior end of the parasphenoid is broad (less pointed than in *Hyla foliamorta*). The pterygoid is slender and well developed.

Natural History.—*Hyla boulengeri* inhabits humid lowland tropical forests and breeds in temporary ponds. Claspings pairs and gravid females were observed at Puerto Viejo, Heredia Province, Costa Rica, on June 21, 1966. Males were calling from depressions in decaying logs and stumps, in forked stems, and from leaves of broad-leaved plants near the pond. Males were observed in late July and early August calling from *Calathea* and *Heliconia* leaves at the edge of a pond in the wet forest of the Osa Peninsula. William E. Duellman informed me that he collected calling males in January at El Real, Darién, and in March at Almirante, Bocas del Toro, Panamá. Taylor (1952) found calling males in June at Turrialba, Cartago Province, Costa Rica, and Dunn (1931a) observed males calling in July, November, and December in Panamá. Gravid females have been found from April to August. Breeding activities of *Hyla boulengeri* always seem to be associated with temporary ponds; in Central America breeding apparently takes place throughout most of the year.

The mating call of *Hyla boulengeri* consists of one short, moderately low-pitched note. Each note has a duration of 0.24 to 0.47 second and is repeated at intervals of one second to several minutes. The notes have 80 to 120 pulses per second, a fundamental frequency of about 70 cycles per second, and a dominant frequency of 2,840 cycles per second (Table 2, Pl. 3A).

The eggs are deposited in a mass in the water. No information is available concerning early development. Tadpoles in advanced stages of development were found in a temporary pond at Rincón de Osa, Puntarenas Province, Costa

Rica. The pond was about 10 cm. deep, had a muddy bottom and lacked vegetation. Three recently metamorphosed young were found in mid-August, 1966, on grass at the edge of another temporary pond in the forest.

Tadpoles.—Twelve tadpoles are available. These were collected at Rincón de Osa, Puntarenas Province, Costa Rica. The maximum size represented is 34.0 mm., total length (stage 42 of development).

A typical tadpole in stage 36 of development (KU 104295) has a body length of 12.0 mm., tail length of 20.0 mm., and total length of 32.0 mm. Other characters are as follows: depth of tail equal to length of body; body deeper than wide; distance between eye and nostril equal to that between nostril and tip of snout; mouth anteroventral, upper and lower lips bare; papillae present laterally; tooth rows 2/3; upper rows about equal in length; first upper row slightly, and second upper row widely, interrupted medially; lower rows about equal in length, shorter than upper rows; third lower row containing 5-10 large teeth; beak strong, serrate; spiracle nearer anus than eye; anal aperture not extending to border of ventral fin; caudal musculature slender posteriorly, extending to tip of pointed tail; dorsal fin extending to middle of body, slightly deeper than ventral fin; posterior three fourths of tail spotted; rest of tail and body gray-brown or transparent; hindlimbs flecked or spotted with brown (Table 3, Fig. 2A and 3A).

TABLE 3.—Sizes of Tadpoles of *Hyla Boulengeri* in Relation to Developmental Stages. (Means in parentheses below observed ranges; measurements in mm.)

Stage	N	Body length	Tail length	Total length
30.....	1	11.0	22.2	33.2
35.....	1	11.0	12.0	23.0
36.....	3	9.5-12.0 (11.2)	20.0-21.5 (20.5)	31.0-32.0 (31.7)
38.....	2	11.5	22.0	33.5
42.....	2	10.5-13.0 (11.8)	21.0-22.0 (21.5)	32.5-34.0 (33.3)
44.....	2	14.0-15.0 (14.5)	8.0-15.0 (12.5)	22.0-30.0 (26.0)
46.....	1	15.0	15.0

A recently metamorphosed young has a snout-vent length of 15 mm.; the head is as long as wide, the eyes are prominent; the limbs are weakly barred; the skin is rugose above and granular below. The venter is immaculate; the dorsum and limbs are gray-brown in preservative (pale green in life). The interorbital space, supratympanic fold, and scapular region are darker than the rest of the body; the fingers lack webbing; the webbing on the foot is the same as in adults; small metatarsal tubercles are present, but the tarsal fold is absent.

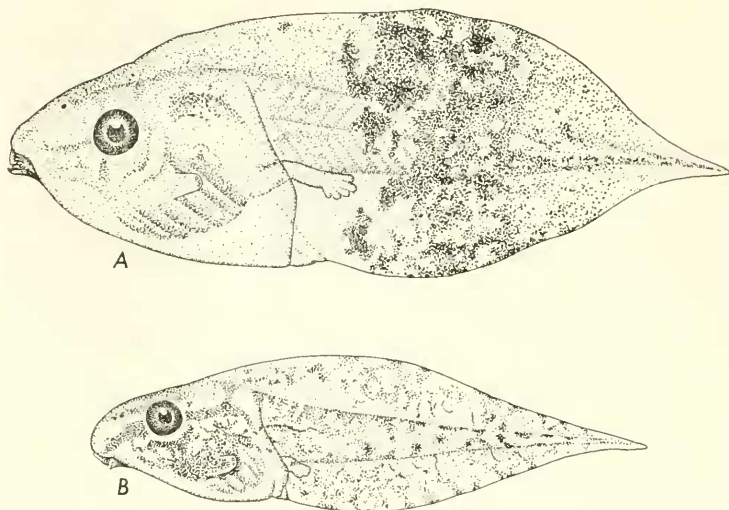


Fig. 2. Tadpoles of (A) *Hyla boulengeri* (KU 104295) and (B) *Hyla elaeochroa* (KU 104134), $\times 3$.

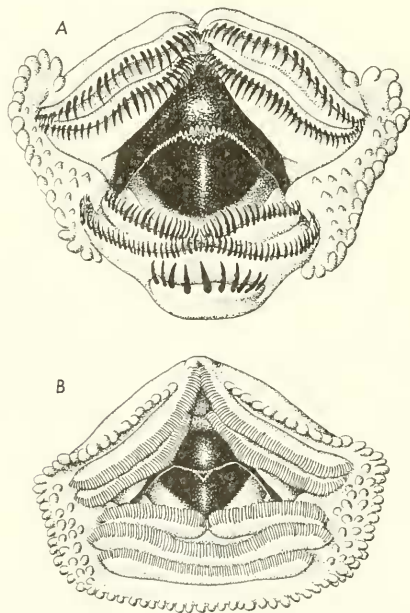


Fig. 3. Mouthparts of tadpoles of (A) *Hyla boulengeri* (KU 104295) and (B) *Hyla elaeochroa* (KU 104134), $\times 25$.

Remarks.—Cope (1887:12) described *Scytotis boulengeri* from Nicaragua. Günther (1901:267) placed *boulengeri* in the genus *Hyla*, and stated that Cope possibly placed *boulengeri* in the genus *Scytotis* on the supposition that it had an accumulation of "sebaceous glands" above the tympanum. Noble (1918:339) redescribed *Hyla boulengeri* on the basis of three specimens from Zelaya Province, Nicaragua, and noted that the glands were not prominent in any of the specimens. Duellman (1956:8) showed that *Scytotis hebes* (generotype of *Scytotis* by monotypy) is a *Phrynohyas*, and thus placed *Scytotis* Cope, 1862, in the synonymy of *Phrynohyas* Fitzinger, 1843.

Dunn and Emlen (1932:25) placed *Hyla lancasteri* Barbour in the synonymy of *Hyla boulengeri*; the former was known solely from one juvenile. They made no qualifying statements, but probably they were impressed by the strongly barred thighs, a coloration known among Central American hylids at that time only in *Hyla boulengeri* (Duellman, 1966a:271). Taylor (1952:856) followed Dunn and Emlen with reservation and noted some differences. Duellman (1966a:271) showed that the holotype of *lancasteri* was a juvenile of a species subsequently named as *Hyla moraviaensis* by Taylor (1952:865).

In Central America, *Hyla boulengeri* can be confused only with *Hyla foliamorta*; the latter is restricted to central and eastern Panamá and northern Colombia. The snout of *foliamorta* is more pointed and protruding, and the vocal sac is darker than in *boulengeri*; the groin of *foliamorta* usually is creamy white, whereas *boulengeri* usually has a dark spot. The skulls differ in that *boulengeri* has a frontoparietal fontanelle, the prevomer is larger and elongate, anteriorly connected to the premaxillary, and posteriorly separated from the sphenethmoid by cartilage; *foliamorta* lacks a fontanelle, the prevomer is smaller, anteriorly separated from the premaxillary by cartilage, but connected by a bony suture to the sphenethmoid. The mating call of *boulengeri* differs by having shorter notes, twice as many pulses per second, a higher fundamental frequency, and more closely approximated major frequencies than does that of *foliamorta*.

Hyla boulengeri need not be compared in detail with the other Central American members of the *Hyla rubra* group, because all of them are smaller and have shorter snouts, smoother skin, and dissimilar color patterns.

Distribution.—In Central America *Hyla boulengeri* inhabits the forested lowlands in locally humid areas in Guanacaste Province, Costa Rica, and in the humid Golfo Dulce region of Costa Rica; it occurs on the Caribbean lowlands from central Nicaragua to South America, where it ranges to Guyana and Ecuador. The highest elevations where *H. boulengeri* has been found are 620 meters at Turrialba, Cartago Province, and 700 meters at Tilarán, Guanacaste Province, Costa Rica (Fig. 4).

Specimens Examined.—Costa Rica: *Alajuela*: 9 km N Ciudad Quesada, near La Florencia, USC 8059 (4); 18 km N Florencia, USC 2624; Laguna Monte Alegre, KU 64334; Las Playuelas, 11 km S Los Chiles, USC 7216, 7217 (2), 7219; 3 km NE Muelle del Arenal, USC 2644 (5). *Cartago*: Turrialba, KU 24741. *Guanacaste*: 7 km N Liberia, USC 8096 (2), 8138 (6); 13.6 km N Liberia, USC 8151, 8171 (2); 20.5 km S Liberia, USC 8205; Taboga, 20 km SE Las Cañas, KU 102170, USC 7166; 4 km NE Tilarán, USC 8023; 6 km NE Tilarán, USC 523 (3), 6262, 7019. *Heredia*: Puerto Viejo, KU 64323-7 (skeletons), 104351-3 (skeletons), 64330-3, 103592-620; 1 km NE Puerto Viejo, UMMZ 126042; 1 km S Puerto Viejo, KU 84983-4 (skeletons), 86317-22, 87774 (skeleton); 4.2 km W Puerto Viejo, KU 64329, 64328 (skeleton). *Limón*: Mountain Cow Creek, near Banano, KU 37031, 41067 (skeleton); 3 km S Río

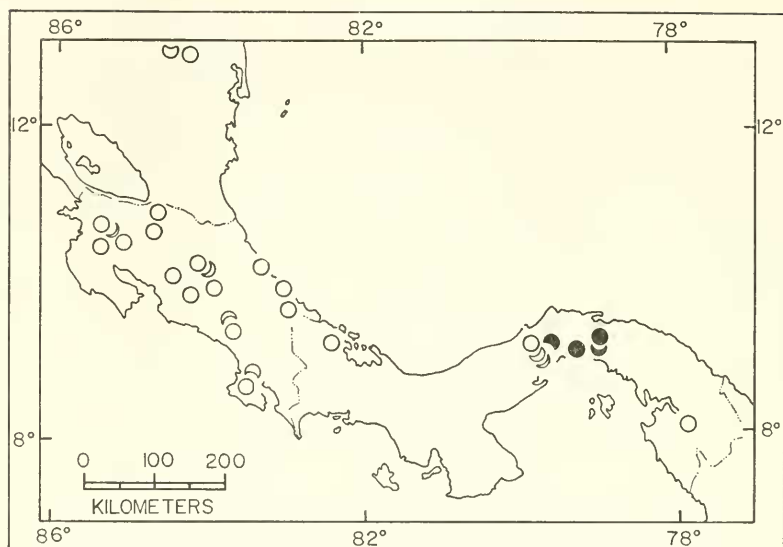


Fig. 4. Map showing locality records for *Hyla boulengeri* (circles) and *H. foliamorta* (dots).

Tortuguero, AMNH 69057; Suretka, KU 36482-8, 36699. *Puntarenas*: 4.8 km S Bahía Rincón on NW side Río Rincón, USC 705; Parrita, USC 6163; 4.5 km W Rincón de Osa, KU 102177-9, 104295-6 (tadpoles); 6 km SW Rincón de Osa, KU 102171-6; 4.4 km NW Villa Neilly, USC 8003; 10.5 km WNW Villa Neilly, KU 64321. *San José*: 21 km WSW San Isidro el General, KU 34104-6.

Panamá: *Bocas del Toro*: 3.2 km W Almirante, KU 95978. *Canal Zone*: Barro Colorado Island, FMNH 13379; near Clayton Reservation, UIMNH 42000; 2.6 km SW Fort Kobbe, KU 95977; Mirofiores Locks, AMNH 69764-5; Summit, AMNH 73445, KU 97777, 101540-9, 104350 (skeleton). *Colón*: Río Gatuncillo, near Nuevo San Juan, KU 95976. *Darién*: El Real, KU 80451-3.

Hyla foliamorta Fouquette

Hyla foliamorta Fouquette, *Herpetologica*, 14:125, April 25, 1958 [Holotype. —TNHC 23109, 11 km. NW Miraflores Locks, Canal Zone, Panamá; M. J. Fouquette, Jr. collector].

Diagnosis.—Size medium (♂ to 43 mm., ♀ to 41 mm.); skull longer than wide; frontoparietal fontanelle absent; snout acuminate, projecting; interorbital triangle bordered by white lines; scapular region having two or more elongate spots; dorsum smooth; vocal sac dark gray; groin creamy white; traces of web between fingers.

Description.—Head flattened, longer than wide; snout flat, pointed, protruding beyond lower lip; loreal region slightly concave; canthus moderately prominent; eyes smaller than interorbital space; tympanum distinct, 55 to 75 per cent of diameter of eye, smaller than internarial space; arms short; fingers having rudimentary webs; median palmar tubercle tripartite; inner palmar tubercle on base of first finger flat; subarticular tubercles distinct; discs of fingers smaller than diameter of tympanum; legs long; tarsal fold lacking;

inner metatarsal tubercle larger than outer; one phalanx free on second, third, and fifth toes, two and one half phalanges free on fourth toe; narrow fringe continuing from web to discs of toes; discs of toes about the size of those on fingers; skin smooth on dorsum and flanks, that on belly and posterior part of thighs granular; tongue oval, longer than wide; vocal slits oblique, about one half length of tongue.

In life, dorsum pale tan to pale reddish brown with irregular reddish brown markings; small dark spots on head; distinct dark brown triangular mark between eyes, bordered by thin white lines; apex of triangle always directed backward; supratympanic fold with black edge; scapular region having two to five small, elongate black spots; belly creamy tan with small brown spots; vocal sac uniformly dark brown with scattered creamy tan flecks; upper jaw dark brown; limbs creamy white below with scattered brown spots; groin marked with small brown spots in some specimens; anterior and posterior surfaces of thighs yellow-orange with three distinct black blotches; two dark bands on upper surface of shanks; webbing of feet yellowish tan with brown mottlings (Pl. 1B).

In preservative, dorsum brown or gray with darker markings; interorbital triangle distinct, bordered by white lines; supratympanic fold with black edge; two or more small elongate black spots in scapular region; belly white with numerous brown flecks; edge of upper lip dark brown; vocal sac dark gray; undersides of limbs creamy white; groin creamy white with or without brown spots; anterior and posterior surfaces of thighs having three black blotches separated by creamy white spaces; shanks having two brown bands; webbing of feet mottled with brown.

Variation.—Twenty-eight breeding males from the area between Chepo and Tocumen, Panamá, have snout-vent lengths of 39.0 mm. to 46.0 mm. (mean 42.5 mm.). In these specimens, the ratio of the tibia length to the snout-vent length is 0.54 to 0.61 (mean, 0.57); the ratio of the diameter of the tympanum to that of the eye is 0.55 to 0.75 (mean, 0.67). One female has a snout-vent length of 41.0 mm., tibia/snout-vent length ratio of 0.57, and tympanum/eye ratio of 0.76. Two to five (usually three) elongate black spots are present in the scapular region in different individuals. The flanks in some are spotted with brown; in others they are creamy white. A small black spot is present in the groin of some specimens. Usually two to four blotches are present on the anterior and posterior surfaces of the thighs; in some specimens the blotches are reduced to small spots. One or two brown spots are present proximally on the shanks in most specimens. In some individuals tuberculations are scattered on the head and in the tympanic and scapular regions, but the dorsum is smooth in most specimens; the belly is creamy white flecked with brown.

Cranial Osteology.—The skull of *Hyla foliamorta* is flat and longer than it is wide. The premaxillary is small and bears 13 to 16 teeth (mean for 2 specimens, 14.8). The alary process of the premaxillary is vertical and concave posteriorly. Ventrally, the premaxillary is completely separated from the prevomer by cartilage. The maxillary is slender; each bears 77 to 84 teeth (mean for 2 specimens, 81). The pars facialis of the maxillary is laterally convex and less than three times the height of the pars dentalis.

The nasal is large and pointed anteriorly and posteriorly in dorsal view.

The length of the nasal comprises about 40 per cent of the total length of the skull. The nasals are separated anteromedially by the cartilaginous septum nasi. One protuberance is present on the midlateral concavity of the nasal. Posteriorly, the nasal overlaps the sphenethmoid; posterolaterally the nasal articulates with the palatine. The sphenethmoid is completely ossified and pentagonal in dorsal view. The frontoparietal is elongate, without a pronounced anterior supraorbital process. The frontoparietals are sutured medially throughout their lengths; the frontoparietal fontanelle is absent.

The bony part of the proötic is narrowly separated dorsolaterally from the squamosal by the cartilaginous crista parotica. The squamosal is large; the anterior arm is pointed. The posterior arm of the squamosal is broad, rounded terminally, and articulates with the proötic medially.

The prevomer is short and separated anteriorly from the premaxillary and maxillary by cartilage. The posterior margin of the prevomer has a bony articulation with the sphenethmoid. Each prevomer bears five to seven teeth. The palatine is small and edentate. The anterior end of the parasphenoid is narrow (more pointed than in *Hyla boulengeri*). The pterygoid is slender and well developed (Fig. 5A).

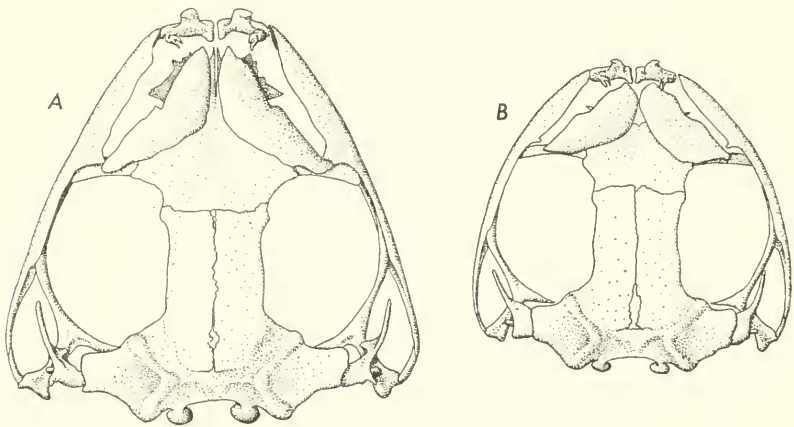


Fig. 5. Dorsal views of the skulls of (A) *Hyla foliamorta* (KU 77687) and (B) *H. elaeochroa* (KU 68259), $\times 3$.

Natural History.—*Hyla foliamorta* inhabits lowland forests in eastern Panamá and breeds in temporary ponds. Males have been observed calling from grasses, bushes, and emergent vegetation near temporary ponds and ditches along roads. William E. Duellman informed me that he found a breeding congregation of this species in June near Chepo, Panamá, where males were calling from spiny palms at the edge of a woodland pond. Fouquette (1958) found calling males in May, August, and September near Miraflores Locks, Canal Zone. Calling stations vary from one to two meters above ground. No clasping pairs have been found; only one female is known (KU 101589, from 8 km NE Tocumen, Panamá); this gravid individual was collected in early June.

The mating call of *Hyla foliamorta* consists of one pulsed, low-pitched, moderate trill of about 0.5 second duration. Each note is repeated at intervals of 5 seconds to a few minutes. The notes have about 50 pulses per second, a fundamental frequency of 56 cycles per second and a dominant frequency of about 3000 cycles per second (Table 2, Pl. 3B).

Egg deposition sites are unknown. No information is available concerning early development, and little is known about the breeding season of *Hyla foliamorta*. Probably its breeding activities are restricted to the rainy months.

Tadpoles.—Eight tadpoles were collected from a weedy temporary pond near Chepo, Panamá, in early June.

A typical tadpole in stage 35 of development (KU 104244) has a body length of 9.5 mm., tail length of 25.0 mm., and a total length of 34.5 mm. Other characters are as follows: depth of tail equal to length of body; body deeper than wide; distance between eye and nostril equal to distance between eye and spiracle; mouth anteroventral; median part of upper lip bare; rest of lip having one row of papillae; a few other rows of small papillae at corners of mouth; tooth rows 2/3; first upper row entire, second upper row interrupted medially, shorter than first; lower rows shorter than upper rows, third shortest; beak moderately robust; spiracle nearer eye than anus; anal tube short, aperture not extending to border of ventral fin; caudal musculature slender, extending to tip of pointed tail; dorsal fin extending onto body (Table 4).

TABLE 4.—Sizes of Tadpoles of *Hyla foliamorta* in Relation to Developmental Stages. (Means in parentheses below observed ranges; measurements in mm.)

Stage	N	Body length	Tail length	Total length
25.....	2	5.0-5.2 (5.1)	8.0-8.5 (8.3)	13.0-13.7 (13.4)
26.....	3	7.0-7.5 (7.2)	12.0-12.4 (12.1)	17.0-19.5 (18.6)
28.....	2	6.5-7.0 (6.8)	18.0	25.0
35.....	1	9.5	25.0	34.5

In life, yellow above, white below; caudal fin greenish yellow with black or gray reticulations; dark line from snout to eye; dark spot behind eye; tail unpigmented except for fine dark reticulations. In preservative body creamy white, transparent below with dark pigment above in some specimens.

Remarks.—*Hyla foliamorta* can be confused only with *Hyla Boulengeri*. The differences between adults of these species were discussed in *Remarks* on *H. Boulengeri*. The tadpoles of *foliamorta* have labial papillae on the lower lip and a stripe between the eye and the tip of the snout. By comparison the tadpoles of *Boulengeri* have a bare lower lip and no stripe between the eye and the tip of the snout.

Distribution.—*Hyla foliamorta* inhabits the subhumid Pacific lowlands

(elevations of less than 100 meters) of Central Panamá and Caribbean lowlands of northern Colombia (Fig. 4).

Specimens Examined.—Panamá: Panamá: 3 km WSW Chepo, KU 77164-9, 101573-5, 104243-4 (tadpoles); 6 km WSW Chepo, KU 77170, 101576-8; 1.5 km SW Naranjal, KU 77171, 77687 (skeleton); 2 km N Tocumen, KU 101579-83, 104349 (skeleton); 8 km NE Tocumen, KU 101584-92.

No specific locality: TNHC 24401.

Hyla rubra Laurenti

Hyla rubra Laurenti, Synopsis Reptilium Emendatum, p. 35, 1768. Daudin, Hist. Nat. Rainettes Grenouilles Crapauds, II:26, 1802. Daudin, Hist. Nat. Particuliere Reptiles, 8:53, 1803. Günther, Catalogue Batrachia Salientia Brit. Mus., p. 110, 1859. Boulenger, Catalogue Batrachia Salientia s. Ecaudata, p. 403, February 1, 1882. Dunn, Occas. Papers, Boston Soc. Nat. Hist., 5:413, October 10, 1931.

Hyla elaeochroa (part): Dunn and Emlen, Proc. Acad. Nat. Sci. Philadelphia, 84:25, March 22, 1932.

Diagnosis.—Size medium; skull longer than wide; frontoparietal fontanelle absent in adults; snout subovoid; choanae rounded; dorsal stripes present; black vermiculations on posterior surfaces of thighs.

Description.—Head flat, longer than wide; snout long, subovoid, slightly protruding beyond lower lip; loreal oblique, concave; canthus rounded, indistinct; diameter of eye about equal to interorbital space; tympanum large, about three fifths diameter of eye, smaller than internarial distance; supratympanic fold indistinct; arms short; fingers free of webs; subarticular tubercles distinct; median palmar tubercle large, bifid; inner palmar tubercle on base of first finger flat, elongate; disc of third finger about one half diameter of tympanum; legs moderately long; tarsal fold absent; inner metatarsal tubercle distinct, oval; toes about half webbed; web on fourth toe extending to disc; discs of toes about size of those on fingers; skin smooth above with small granules on head and in scapular region in some specimens; skin on flanks, throat, belly, and lower surfaces of thighs granular; tongue oval, longer than wide, not free behind; choanae small, oval; vocal slits long, lateral to tongue.

In preservative, dorsum pale brown with darker dorsolateral stripes; narrow dark brown line from nostril to eye; groin, anterior surface of thighs, and posteroventral surfaces of shanks creamy tan with dark brown vermiculations; white spots present on thighs in some specimens; throat flecked with brown; belly creamy white or gray.

Remarks.—The taxonomic history of *Hyla rubra* Laurenti is confused. Seba (1734:70) illustrated and diagnosed a frog for which he used the name *Ranula, Americana, Rubra*. Linnaeus (1758:213) considered Seba's frog to be a variety of *Hyla arborea*. Laurenti (1768:35) apparently examined the same individual that Seba called *Ranula, Americana, Rubra*. For this specimen, Laurenti used the binominal *Hyla rubra* and provided a brief diagnosis. The type locality was given as America.

Daudin (1802:26) redescribed the same specimen(s?) treated by Seba and Laurenti and provided a fairly good description and figures. Daudin restricted the type locality to Surinam and indicated that Marin de Baize was the probable collector. Daudin (1802:26 and 1803:53) neglected to consider Laurenti's work, but he applied the same name used by Laurenti. Most authors have

credited *Hyla rubra* to Daudin, but Rivero (1961:120) noted that *Hyla rubra* Laurenti, 1768, has priority over *Hyla rubra* Daudin, 1802. Since both Laurenti and Daudin worked on Seba's material, it is reasonable to assume that Daudin redescribed the same frog that was named by Laurenti; this was not an uncommon practice in the early nineteenth century. Thus I conclude that *Hyla rubra* Daudin, 1802, is a junior synonym of *Hyla rubra* Laurenti, 1768.

Dunn (1931a:413) first reported *Hyla rubra* from Central America; he recorded the species from the Canal Zone and San Pablo, Panamá. I have examined the material of *Hyla rubra* from Panamá deposited in various museums. Most of the specimens are faded, discolored, and do not have distinct brown vermiculations on the thighs. The specimens seem to be more like *Hyla rubra* than any of the other species in the *rubra* group. The presence of oval choanae and a tympanum larger than the largest finger disc separate these specimens from *Hyla elaeochroa*, a species with which *rubra* has been confused. *Hyla elaeochroa* does not occur in the Canal Zone or eastern Panamá. All museum specimens from Nicaragua, Costa Rica, and western Panamá that have been called *Hyla rubra*, plus those mentioned by Dunn and Emlen (1932:25) and Dunn (1933:61) are *Hyla elaeochroa*.

The taxonomic status of the many South American populations referred to *Hyla rubra* and of other populations now recognized as different species is not clear at the present time. Considerable variation in external characters and in cranial features has been observed in South American *rubra*. A review of the taxonomy of these populations is beyond the scope of this paper. Possibly the Central American specimens herein referred to *rubra* will ultimately be found to be specifically distinct from those in Surinam. Since I have no osteological material from Central America, I have been unable to describe the cranium in this account. Furthermore, I have no data on the ecology and life history of *rubra* in Central America.

Distribution.—*Hyla rubra* inhabits lowland tropical forests from central-eastern Panamá to northern South America and thence through lowlands east of the Andes to northern Argentina (Fig. 6).

Specimens Examined.—Panamá: Canal Zone: Gatun, UMMZ 52720 (2); Madden Dam, FMNH 67820; no specific locality, UMMZ 56517 (3), USNM 37863. Colón: Cerro Bruja, MCZ 13248. Darién: El Real, USNM 140569-70, 140573. Panamá: Juan Díaz, MCZ 17973; Las Sabanas, MCZ 17581; Río Trinidad, UMMZ 64003; San Pablo, MCZ 1398-9.

Hyla elaeochroa Cope

Hyla elaeochroa Cope, Jour. Acad. Nat. Sci. Philadelphia, 8:105, 1876 [Holotype.—USNM 30689, Sipurio, Limón Province, Costa Rica; William M. Gabb collector]. Günther, Biologia Centrali-Americana, Reptilia and Batrachia, p. 265, June 1901. Taylor, Univ. Kansas Sci. Bull., 35:859, July 1, 1952. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 17:270, June 17, 1966.

Hyla quinquevittata Cope, Proc. Amer. Philos. Soc., 23:273, April 1887 [Holotype.—USNM 14187, Nicaragua; J. F. Bransford collector]. Günther, Biologia Centrali-Americana, Reptilia and Batrachia, p. 268, June 1901. Noble, Bull. Amer. Mus. Nat. Hist., 38:340, June 1918.

Hyla rubra (part): Dunn and Emlen, Proc. Acad. Nat. Sci. Philadelphia, 84:25, March 22, 1932.

Hyla dulcensis Taylor, Univ. Kansas Sci. Bull., 39:37, November 18, 1958 [Holotype.—KU 32168, Golfito, Puntarenas Province, Costa Rica; Edward H. Taylor collector].

Diagnosis.—Size medium (♂ to 38 mm., ♀ to 40 mm.); skull wider than long; nasals truncate anteriorly; frontoparietal fontanelle moderate in size; snout slightly protruding; tympanum about size of largest discs on fingers; dorsum marked by longitudinal stripes; dark stripe between eye and nostril; in life tan to olive-green with or without dark mark between eyes; bones greenish blue.

Description.—Head flat, longer than wide; snout long, rounded, protruding beyond mouth; canthus indistinct; length of eye equal to interorbital distance; loreal region not pronounced; tympanum distinct and about two-fifths diameter of eye; interorbital triangle present or absent; arms short; trace of web between fingers, extending as fringe along sides of fingers; first finger very short with small disc; other discs about size of those on toes; discs on third finger and fourth toe as large as tympanum; outer palmar tubercle moderate in size, partly bifid; inner palmar tubercle large, elongate, flat; subarticular tubercles distinct; legs moderately long; tarsal fold absent; inner metatarsal tubercle flat; outer metatarsal tubercle smaller, indistinct; subarticular tubercles moderate in size; fringe on toes to tip of disc of second toe; rest of toes about two-thirds webbed; foot length about two fifths snout-vent length; tibia length about one half snout-vent length; skin above smooth or with minute pustules; belly finely granular; ventral surfaces of thighs and areas below anus granular; skin on ventral surfaces of limbs smooth; tongue relatively large, longer than wide, barely notched behind; vocal slits elongate, lateral to tongue; choanae medium in size. In life, dorsum yellowish brown, olive green, or grayish brown with dark brown spots on snout, dark brown stripe from nostril to eye, dark yellow-brown interorbital triangle, and dark supratympanic region; generally five interrupted longitudinal dark brown stripes on dorsum (one on each flank, pair of paravertebral and one vertebral); flanks pale yellow; groin yellowish brown; thighs marked with one or two transverse yellow-brown blotches; shanks with two or three yellow-brown blotches above; spaces between blotches on thighs, shanks, tarsi, and feet yellow; brown spots on tarsi and in some specimens on feet; arm pale yellow with pale brown spots; belly creamy white having slight blue-green tint; vocal sac and chin yellow; axillary region yellow, blue-green in some specimens (Pl. 2A).

In preservative, head and dorsum yellowish brown; dark brown stripe from nostril to eye; dark brown spots on snout; a dark brown interorbital triangle with apex directed backward; dark brown supratympanic region; dorsal stripes same as in living individuals; flanks pale yellow with brown spots in some specimens; groin creamy white; thighs and shanks having or lacking transverse dark brown blotches; spaces between blotches creamy white or yellow-brown; arms pale yellowish brown; belly and vocal sac creamy white.

Variation.—Geographic variation in size and some proportions, such as the ratio of tibia length to snout-vent length and the ratio of the diameter of the tympanum to that of the eye, have been observed in this species. The largest individuals are from the Golfo Dulce region (samples from Piedras Blancas and Rincón de Osa), Puntarenas Province, Costa Rica. The smallest individuals are from El Recreo, Zelaya Province, Nicaragua, and from the Caribbean lowlands of Costa Rica.

The diameter of the tympanum is proportionately larger (relative to the size of the eye) in males from Tilarán, Guanacaste Province; the tympanum

is nearly as large in males from Piedras Blancas, Puntarenas Province, and Puerto Viejo, Heredia Province, Costa Rica. The lowest ratios occur in individuals from Almirante, Bocas del Toro, Panamá, in specimens from the Caribbean lowlands of Costa Rica (except Puerto Viejo), and in those from El Recreo, Zelaya Province, Nicaragua. In general, the tympanum is proportionately larger in females than in males; the tympanum is largest in females from the Pacific lowlands of Costa Rica (Table 5).

Color variation has been observed in individuals from the same population, as well as in individuals from different localities, between males and females, and from night to day. In life, most individuals from the Pacific lowlands of Costa Rica are dark tan to greenish gray above with dark brown longitudinal stripes that are entire or broken, but some specimens (mostly males) are dusky brown and lack longitudinal stripes or an interorbital triangle; females usually have the dark interorbital triangle and the stripes on the dorsum. Individuals from Turrialba, Cartago Province, Costa Rica, are pale olive-tan with olive-brown markings. Individuals from Puerto Viejo, Heredia Province, Costa Rica, are uniformly yellowish brown with or without dark longitudinal stripes. Specimens from El Recreo, Zelaya Province, Nicaragua, are like those from Puerto Viejo. Males from Almirante, Bocas del Toro, Panamá, are pale brown with dark brown longitudinal stripes and an indistinct interorbital triangle. Females have a distinct interorbital triangle and dark brown blotches on the thighs and shanks.

By night, the dorsum usually is pale yellow, and the belly is creamy white. By day, the dorsum is dark tan; the stripes and spots are darker, and the belly is yellowish white. Taylor (1952) noticed that considerable variation in color pattern occurred from night to day in individuals from Turrialba, Cartago Province, Costa Rica. At night some individuals lacked a dorsal pattern, but by day many of these individuals developed dorsal stripes.

Cranial Osteology.—The skull of *Hyla elaeochroa* is slightly wider than it is long, and flat. The premaxillary is small and bears 10 to 15 teeth (mean for 9 specimens, 12.3). The alary process of the premaxillary is small, vertical, and slightly concave posteriorly. Ventrally, the premaxillary is partially united to the prevomer by ossification. The maxillary is slender and bears 70 to 82 teeth (mean for 9 specimens, 74.3). The pars facialis of the maxillary is laterally convex and is about twice as high as the pars dentalis.

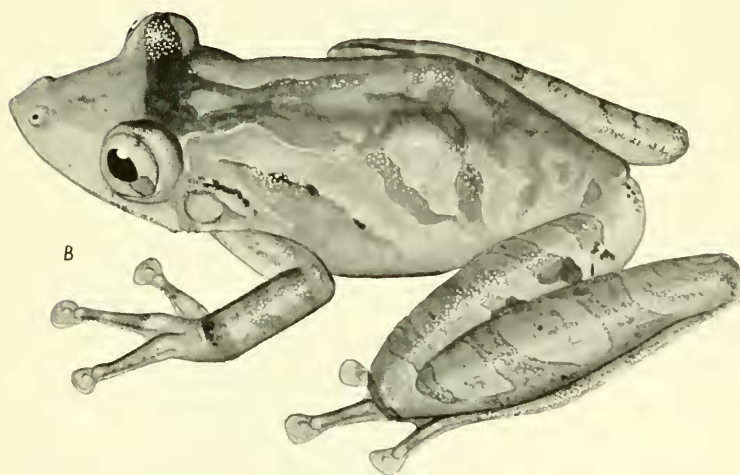
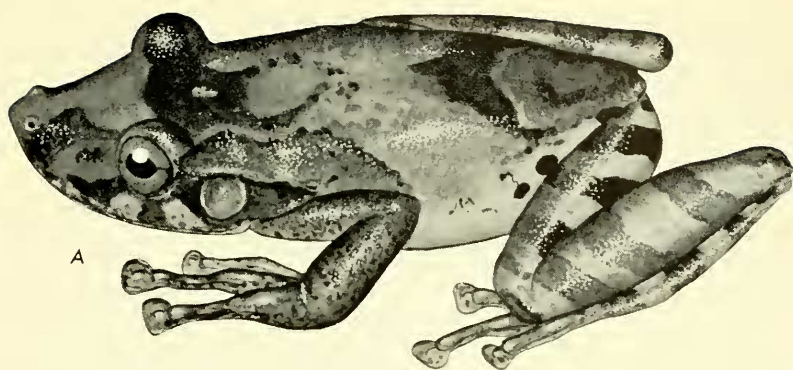
The nasal is large, robust, anteriorly truncate, but pointed posteriorly in dorsal view. The nasal comprises about 45 per cent of the total length of the skull. There is an anterior cartilaginous septum nasi separating the two nasals; the latter overlap the sphenethmoid posteriorly. Each nasal bears a shallow concavity in the midlateral side and lacks a maxillary process. Dorsally, the sphenethmoid is wider than long, roughly pentagonal in shape; the frontoparietal is elongate, smooth, and bears a small anterior supraorbital process. The sphenethmoid and frontoparietal form the anterior margin of the frontoparietal fontanelle; the fontanelle is narrow anteriorly and wider posteriorly (Fig. 5B).

The entire distal surface of the proötic is in contact with the posterior arm of the squamosal. A narrow cartilaginous crista parotica is visible dorsally in some specimens. The squamosal is broad posteriorly but its anterior arm is slender and not in contact with the maxillary.

TABLE 5.—Geographic Variation in Size and Proportions in Males of *Hyla elacochroa*.
(Means in parentheses below observed ranges.)

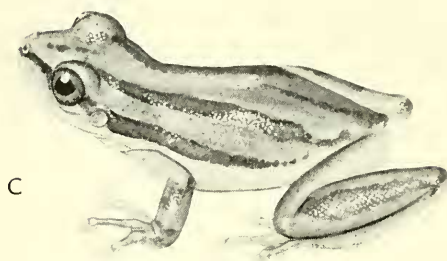
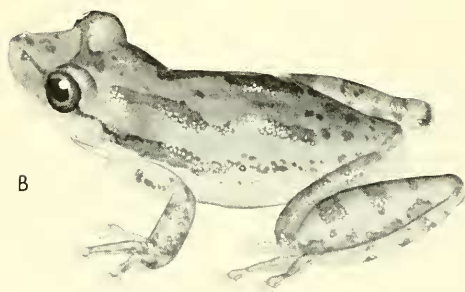
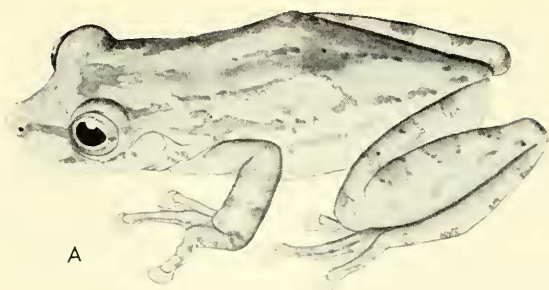
Locality	N	Snout-vent length (mm.)	Tibia length/ snout-vent	Tympanum/ eye	Foot length/ snout-vent
Nicaragua: El Recreo.....	9	28.0-30.3 (29.3)	0.51-0.57 (0.55)	0.47-0.59 (0.51)	0.39-0.54 (0.41)
Costa Rica: Tilarín.....	21	28.8-33.6 (30.6)	0.47-0.57 (0.52)	0.48-0.65 (0.59)	0.40-0.46 (0.41)
Costa Rica: Puerto Viejo.....	22	26.3-32.4 (29.7)	0.49-0.54 (0.52)	0.48-0.65 (0.57)	0.38-0.45 (0.42)
Costa Rica: Turrialba.....	95	28.1-35.0 (30.6)	0.47-0.56 (0.51)	0.47-0.68 (0.56)	0.37-0.46 (0.41)
Costa Rica: Bataán, Limón, and Suretka.....	26	26.3-32.7 (30.0)	0.47-0.54 (0.51)	0.45-0.66 (0.50)	0.36-0.44 (0.41)
Costa Rica: Piedras Blancas....	21	33.3-37.7 (35.2)	0.50-0.54 (0.51)	0.48-0.64 (0.57)	0.40-0.46 (0.43)
Costa Rica: Rincón de Osa.....	24	31.4-35.9 (34.1)	0.50-0.56 (0.53)	0.45-0.61 (0.54)	0.40-0.46 (0.43)
Panamá: Bocas del Toro.....	6	31.0-33.5 (32.1)	0.49-0.54 (0.51)	0.47-0.50 (0.48)	0.41-0.43 (0.42)

PLATE 1



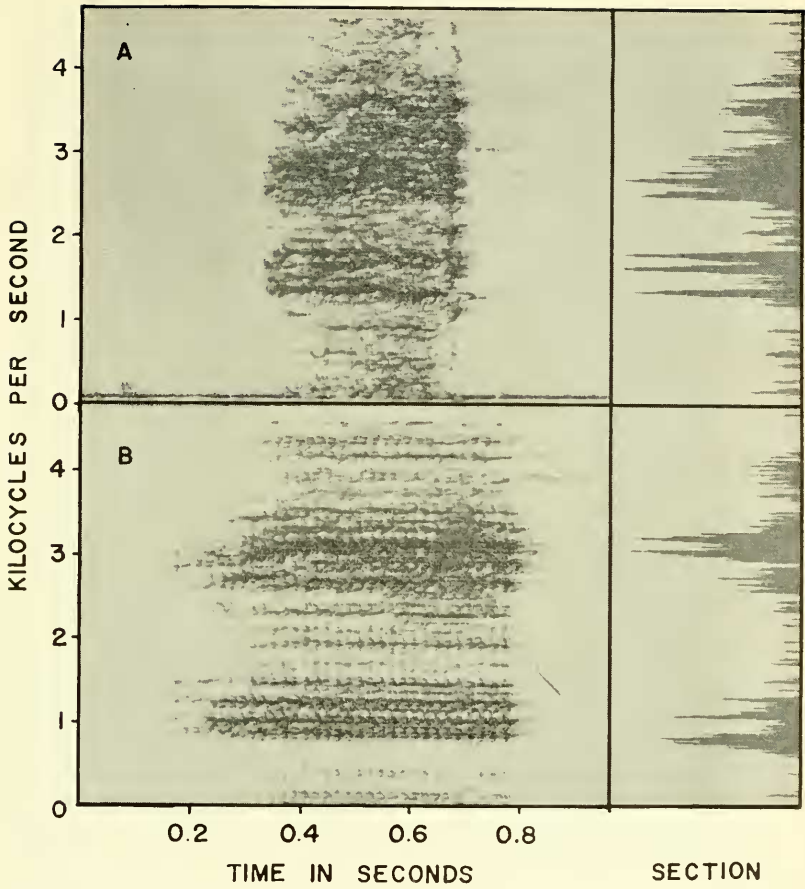
Living *Hyla*: (A) *H. boulengeri* (KU 86322) and (B) *H. foliamorta* (KU 101576), $\times 2$.

PLATE 2



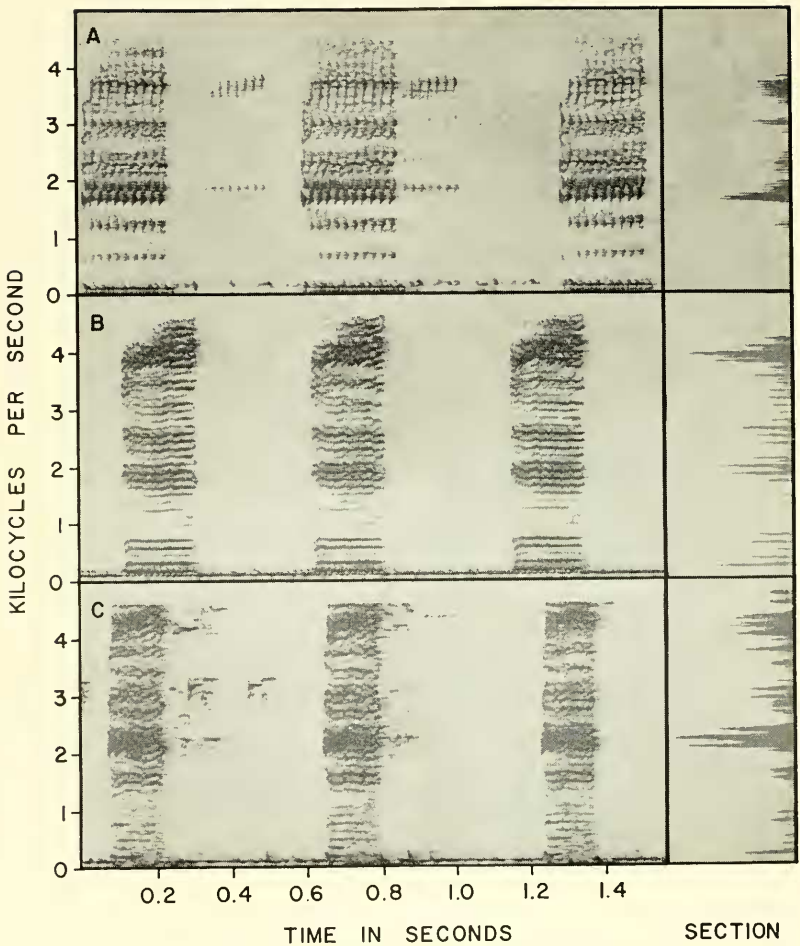
Living *Hyla*: (A) *H. elaeochroa* (KU 91688), (B) *H. staufferi staufferi* (KU 57791), and (C) *H. staufferi altae* (KU 101688), $\times 2$.

PLATE 3



Audiospectrograms and sections of mating calls of (A) *Hyla boulengeri* (KU Tape No. 511) and (B) *Il. foliamorta* (KU Tape No. 288).

PLATE 4



Audiospectrograms and sections of mating calls of (A) *Hyla elaeochroa* (KU Tape No. 97), (B) *H. s. staufferi* (KU Tape No. 93), and (C) *H. staufferi altae* (KU Tape No. 502).

The prevomer is short, and broadest anteriorly. The prevomer is joined to the premaxillary by ossification. The posterior margin of the prevomer bears a narrow cartilaginous articulation with the sphenethmoid. The antero-lateral and posterolateral processes of the prevomer form an incomplete bony margin to the small choanae; each prevomer bears four to seven teeth. The palatine is small, curved anteriorly and edentate. The anterior part of the parasphenoid is robust and ends in a point. The pterygoid is slender and weakly developed.

Natural History.—*Hyla elaeochroa* inhabits humid lowland tropical forests in lower Central America and breeds in temporary ponds. Clasping pairs, gravid females, and calling males have been found mostly in June, July, and August. William E. Duellman informed me that he also found males calling in mid-February, late April, and May. Duellman (1967) reported detailed observations of the social organization in the mating call of *Hyla elaeochroa*. The choruses in this species are initially organized, but when many individuals call, the chorus loses organization. I observed this species breeding in a temporary pond at Puerto Viejo, Heredia Province, Costa Rica, in late June. Calling males and clasping pairs were extremely abundant within a few hours after a heavy rain. Males were mostly found calling from low emergent herbs in the pond and less commonly from bushes and trees to heights of six meters above the water. Calling males were also observed at Rincón de Osa, Puntarenas Province, Costa Rica, in late July. These breeding individuals were found in a shallow pond at the edge of a wet forest. Calling stations were less than two meters in height. John D. Lynch informed me that after a heavy rain in early August, he found several hundred individuals congregated in a small grassy pond less than a foot deep, at Rincón de Osa. Males were calling from sites on grass stems a few centimeters above the water.

The mating call of *Hyla elaeochroa* consists of short notes, repeated at intervals of about 0.40 second. Each note has a duration of 0.12 to 0.24 second. The fundamental frequency varies from 48 to 65 cycles per second, and the notes have 40-50 pulses per second; the dominant frequency is at about 2,900 cycles per second (Table 2, Pl. 4A).

The eggs are deposited in a mass in the water near floating vegetation. William E. Duellman informed me that he observed hatchlings oriented vertically with the tip of the mouth at the surface of the water. They gradually sank to bottom, but swam back to surface again. No additional information is available concerning early development. Tadpoles have been found in shallow grassy ponds in clearings and in temporary woodland ponds.

Tadpoles.—Three hundred and thirty-one tadpoles in various stages of development are available. Thirty-five tadpoles in stage 35 have a mean body length of 8.1 mm. (8.0-9.0 mm.), tail length of 17.7 mm. (15.0-19.5 mm.), and total length of 25.9 mm. (23.0-27.5 mm.). The largest tadpole examined is in stage 40 and has a total length of 34.5 mm. (Table 6).

A typical tadpole, stage 35 of development (KU 104134, from Puerto Viejo, Heredia Province, Costa Rica), has a body length of 9.1 mm., tail length of 17.7 mm., and a total length of 26.8 mm. Other characters are as follows: body depressed anteriorly; body length greater than depth of tail; internarial space as broad as interorbital distance; nostril equidistant between eye and tip of snout; eyes moderately large; mouth anteroventral and triangular; median

TABLE 6.—Sizes of Tadpoles of *Hyla elaeochroa* in Relation to Developmental Stages. (Means in parentheses below observed ranges; measurements in mm.)

Stage	N	Body length	Tail length	Total length
24.....	2	4.0-4.0 (4.0)	8.5-9.0 (8.8)	12.5-13.0 (12.8)
25.....	64	5.0-6.5 (5.7)	8.5-15.0 (11.8)	13.5-21.5 (17.6)
27.....	30	7.0-7.5 (7.1)	13.0-16.0 (14.2)	20.0-23.0 (21.3)
30.....	15	7.0-8.0 (7.3)	13.0-16.5 (15.0)	20.0-24.0 (22.4)
32.....	30	7.5-8.5 (7.8)	15.0-17.0 (16.1)	22.5-25.0 (23.8)
35.....	35	8.0-9.0 (8.1)	15.0-19.5 (17.7)	23.0-27.5 (25.9)
37.....	22	8.5-9.5 (9.0)	16.0-22.0 (18.8)	25.0-31.0 (27.8)
39.....	14	9.5-10.5 (9.9)	19.0-24.9 (21.1)	28.5-33.5 (31.0)
40.....	27	7.0-11.5 (9.1)	15.0-23.0 (22.0)	23.0-34.5 (31.2)
43.....	10	8.0-12.0 (10.2)	11.0-17.0 (13.5)	20.0-26.0 (23.7)
45.....	16	10.0-12.0 (11.2)	1.0-7.0 (3.4)	12.0-17.0 (14.6)
46.....	45	11.0-13.0 (11.8)

fourth of upper lip bare; rest of lip bordered by one row of papillae; clumps of small papillae at corners of mouth; tooth rows 2/3; upper rows equal in length; second row interrupted medially; lower rows shorter than upper rows, diminishing in length; beak rather weak with small serrations; spiracle short and nearer eyes than anus; anal opening not reaching edge of ventral fin; caudal musculature attenuated distally (Figs. 2B and 3B).

In life, dorsum yellowish tan with gray-brown mottling; belly and ventrolateral surfaces silvery-gold or white; black stripe from tip of snout to eye; two black blotches below eye, another blotch extending from eye to base of caudal musculature; caudal musculature and fins gray-brown. In preservative, yellowish tan and silvery-gold colors lost; black reticulations present on tail.

Remarks.—Cope (1876:105) described *Hyla elaeochroa* from Sipurio, Limón Province, Costa Rica. He based his description on a small specimen, 26.0 mm. in snout-vent length, having a dorsum uniformly colored and lacking an inter-

orbital triangle and blotches on the thighs. Cope (1887) described pigmented specimens from Nicaragua as *Hyla quinquevittata*, which he diagnosed as having dark brown bars on the hind limbs and five dark brown longitudinal stripes on the dorsum, the median one of which was expanded anteriorly so as to form a large triangular spot between the eyes. He thought this species was related to *Hyla eximia* Baird and noted that "the hinder legs are much larger; the muzzle is more acuminate and the color bands are much wider" than in *eximia*. Cope did not compare *quinquevittata* with *elaeochroa*, which he had described ten years before. Günther (1901:268), Noble (1918:340), and Nieden (1923:251) regarded both *elaeochroa* and *quinquevittata* as valid species. Dunn and Emlen (1932:25) regarded both as synonyms of *Hyla rubra*, but they made no qualifying statements. Taylor (1952:859) placed *quinquevittata* as a synonym of *elaeochroa* and indicated that *rubra* was another species.

Taylor (1958:37) described *Hyla dulcensis* from the humid tropical forests of Golfo Dulce, Puntarenas Province, Costa Rica. He thought this species was "related to *H. elaeochroa* but differs in its somewhat larger size, smaller finger and toe discs, the obsolete canthus rostralis; the loreal region concave and the choanae larger." Duellman (1966a:270) compared adults, tadpoles, and mating calls of *dulcensis* and *elaeochroa* and concluded that a single species was involved.

Hyla elaeochroa can be easily confused with the closely related *Hyla staufferi*. Although the durations of the calls are similar, the call of *elaeochroa* has only about one third the number of pulses per second, a much lower fundamental frequency, and a lower dominant frequency than that of *staufferi*. *Hyla elaeochroa* is larger and has a less pointed snout than does *staufferi*. Although the skulls of the two species are similar, that of *elaeochroa* differs in having broad palatines and comparatively larger nasals that are truncate anteriorly. In *staufferi* the nasal is rounded anteriorly and the palatine is absent.

Distribution.—*Hyla elaeochroa* occurs on the Caribbean lowlands from western Panamá through Costa Rica to eastern Nicaragua, and on the Pacific lowlands of southeastern Costa Rica and extreme western Panamá. Most localities where it has been collected are below 800 meters, but the species has been found at two localities above 1000 meters (El Silencio and Pacuare, Cartago Province) on the Caribbean slopes of the Cordillera de Talamanca, Costa Rica (Fig. 6).

Specimens Examined.—Nicaragua: Zelaya: El Recreo, UMMZ 79721 (9).

Costa Rica: Alajuela: Laguna Monte Alegre, KU 64499. Cartago: 2 km E Chitaría, KU 107058; El Silencio, 14.4 km NE Turrialba, KU 107059-60; 4.6 km ENE Pacuare, KU 64451-75, 64628-37; 4 km S Pavones, KU 64500; Turrialba (Instituto Interamericano de Ciencias Agrícolas), KU 30305-26, 24616-57, 30337-54, 31776-91, 31803, 31807-15, 64413-50, 68283-87 (skeletons), 68390-1 (young), 35042 (eggs), 25207-8 (skeletons), 25221 (skeleton), 41073-83 (skeletons). Guanacaste: 2 km E Tilarán, KU 86356-77, 87667-8 (young). Heredia: Puerto Viejo, KU 36696, 46466, 64501-17, 68288-91, 68387, 68388-9 (young), 91803 (young), 91688-9, 104134 (tadpoles), 104135 (young), 104354-6 (skeletons); 1.5 km N Puerto Viejo, KU 64518-23, 68386 (tadpoles); 1 km S Puerto Viejo, KU 84985-6 (skeletons), 87669 (young), 87772-3 (skeletons). Limón: Bataán, KU 30327-36; La Lola, KU 64478-98, 68281-2 (skeletons); Los Diamantes, KU 31800-02, 64476-7; Peralta, KU 31816-21; Puerto Limón, KU 31792-99; Suretka, KU 36467-79, 36697, 41084. Puntarenas: 5 km NW Buenos Aires, KU 107057; 10 km E Esparta, KU 87666 (tadpoles); Golfito, KU 32166-8; 8 km E Palmer Norte KU 93939; 10.7 km SE Palmar Sur, KU 93938 (skeleton), 93940-51, 93952 (eggs), 93953-6 (tad-

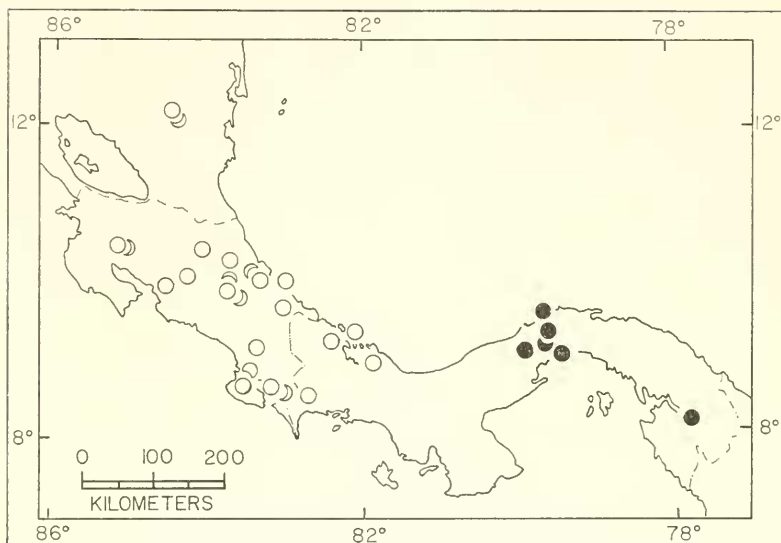


Fig. 6. Map showing locality records for *Hyla elaeochroa* (circles) and *H. rubra* (dots).

poles); Piedras Blancas, KU 103646-59; 4.5 km W Rincón de Osa, KU 102208-41, 104298 (tadpoles).

Panamá: Bocas del Toro: Almirante, KU 80079; Isla Bastimentos, KU 96008-11; Río Cricamola, 3.7 km from coast, KU 96012. Chiriquí: Río Gariché, 8.3 km ESE Paso de Canoas, KU 101571-2.

Hyla staufferi Cope

Hyla staufferi Cope, Proc. Acad. Nat. Sci. Philadelphia, 17:165, October 1, 1865 [Holotype.—USNM 15317, Orizaba, Veracruz, México; Francis Sumichrast collector].

Diagnosis.—Small frogs (♂ to 29 mm., ♀ to 31.6 mm.); skull longer than wide; palatine absent; large cartilaginous crista parotica present; snout flat, elongate and protruding; dark interorbital bar and dorsal stripes usually present.

Description.—Head flat, especially in females, longer than wide; snout long, protruding beyond mouth; loreal region concave; canthus ill-defined; length of eye greater than interocular distance or width of eyelid; length of eye less than interorbital space; tympanum distinct; interorbital spot irregular; supratympanic fold faint; arms short; fingers free of webs; discs on third and fourth fingers equal to diameter of tympanum; inner metatarsal tubercle on base of first finger distinct; first finger shorter than second; palmar tubercle distinct (Fig. 1C); legs short (usually less than 50 per cent of snout-vent length); tarsal fold absent; metatarsal tubercles small, outer tubercle smaller than inner; subarticular tubercles small, simple, distinct; toes less than half webbed (Fig. 1D); skin smooth above with a few small pustules on head, scapular region, flanks, and supratympanic region; arms and legs smooth; skin of belly coarsely granular; posteroventral surfaces of thighs finely granular; tongue small, rounded,

longer than wide, slightly free and notched posteriorly; vocal slits small, lateral to tongue; choanae moderate in size.

Variation.—The largest males of *Hyla staufferi* are from Jalapa, Guatemala, and from San Salvador, El Salvador. In these samples the average snout-vent length is 27 mm. In Panamanian specimens the average snout-vent length is 23.6 mm. Slight variation in the ratio of tibia length to snout-vent length exists throughout the range; more variation exists in the ratio of the diameter of the tympanum to that of the eye; the tympanum is proportionately larger in northern populations (Table 7). The primary differences between Panamanian and more northern populations are in size, color pattern on the dorsum and shanks, amount of webbing between the toes, and duration of notes in the mating call (Table 2, Pl. 4).

The color in Panamanian *staufferi* is gray or gray-brown with a pair of distinct, complete, dark brown dorsolateral stripes, a pair of entire paravertebral stripes, and in some specimens a vertebral stripe. About five per cent of the individuals have interrupted stripes on the dorsum, whereas in the more northern populations complete paravertebral stripes are present in less than ten per cent of the specimens; when complete stripes are present, they are irregular. The dorsal ground color in non-Panamanian specimens is brown, olive-brown, or dark brown.

Transverse bars are present on the shanks in *Hyla staufferi* from Costa Rica northward to México, whereas in Panamá all the individuals have a longitudinal stripe on the shank (Table 7, Pl. 2). The interorbital spot or bar is more noticeable in northern populations than in specimens from Panamá. Frogs from Costa Rica and northward have the toes about three fourths webbed, whereas in Panamá the toes are about two fifths webbed. The mating calls of the northern and Panamanian populations are similar, but the notes have a longer duration in the northern populations and a higher dominant frequency in Panamanian populations.

Hyla staufferi is the most variable member of the *Hyla rubra* group in Central America. The Panamanian populations are geographically separated from the Costa Rican and more northern populations by an area of tropical rainforest in the Golfo Dulce region in southeastern Costa Rica and adjacent Panamá. *Hyla staufferi* does not occur on the Caribbean versant of Costa Rica and Panamá. The Golfo Dulce region and the Caribbean versant are humid and inhabited by *Hyla elaeochroa*. *Hyla staufferi* is an inhabitant of subhumid and xeric areas.

On the basis of the discontinuous variation in several characters which correlate with the disjunct distribution of the two populations, two subspecies of *Hyla staufferi* are recognized. The accounts that follow apply equally to each.

Cranial Osteology.—The skull of *Hyla staufferi* is flat and longer than wide. The premaxillary is small and bears 9 to 13 teeth (mean for 5 specimens, 11.3). The alary process of the premaxillary is small, concave posteriorly and vertical. Ventrally, the premaxillary is united to the prevomers by partially ossified cartilage. The maxillary is slender and usually bears 49 to 70 teeth (mean for 5 specimens, 60.7). The pars facialis of the maxillary is convex and less than twice the height of the pars dentalis.

The nasal is large, rounded anteriorly, and pointed posteriorly in dorsal view. The nasal comprises about 40 per cent of the total length of the skull. Antero-

TABLE 7.—Geographic Variation in Size and Color in Males of *Hyla staufferi*.
(Means in parentheses below observed ranges.)

Locality	N	Snout-vent length (mm.)	Complete dorsal stripes (per cent)	Barred shanks (per cent)
Veracruz.....	47	23.0-27.3 (25.4)	0.0	100
Campeche.....	20	24.6-27.5 (25.5)	0.0	100
Oaxaca.....	75	24.0-28.7 (26.4)	9.3	100
Chiapas.....	20	23.2-27.8 (25.5)	10.0	100
Guatemala.....	22	25.0-29.0 (26.9)	10.9	100
El Salvador....	21	24.7-28.6 (27.0)	0.0	100
Honduras.....	34	20.6-27.0 (24.9)	3.3	100
Nicaragua.....	67	21.5-26.8 (24.9)	3.0	92.7
Costa Rica.....	54	20.7-26.6 (24.2)	5.5	98.1
Total Non- Panamanian	360	20.7-29.0 (25.9)	5.4	98.3
Panamá.....	72	21.7-26.0 (23.6)	94.5	0.0

medially the two nasals converge; posteriorly they overlap the sphenethmoid. The nasals lack a concavity in the midlateral surface. Dorsally, the sphenethmoid is wider than long, roughly pentagonal in shape; the frontoparietal is elongate, narrow, and smooth, with a small supraorbital process anteriorly. The frontoparietal fontanelle is narrow anteriorly and wide posteriorly.

Only a narrow connection exists between the posterior, pointed arm of the squamosal and the lateral edge of the proötic. The crista parotica is visible dorsally along the lateral edge of the bony proötic. The squamosal is narrow anteriorly and posteriorly.

The prevomers are short and separated anteriorly by partly ossified cartilage of the overlying solum nasi. The prevomer is joined to the premaxillary by cartilage. The posterior margin of the prevomer articulates directly with the sphenethmoid. The anterolateral and posterolateral processes of the prevomers form the incomplete bony internal margin of the choanae. Each prevomer

bears three to six teeth. The palatine is absent. The anterior part of the parasphenoid is narrow and ends in a point. The pterygoid is slender and weakly developed.

Natural History.—Throughout its range *Hyla staufferi* occurs in subhumid forests and savannas; consequently, the breeding activities are limited by the seasonal occurrence of rainfall, which accumulates in temporary ponds where this species breeds. Claspings pairs and gravid females have been found mostly from June to August throughout its range. This species was observed calling at Finca Taboga, Guanacaste Province, Costa Rica, in mid-July. The males were calling from temporary grassy and weedy ponds in which *Hyla microcephala* also was calling, but the two species had different calling sites. *Hyla staufferi* called at stations at heights of five to 80 cm. near the edge of the pond, whereas *Hyla microcephala* called from emergent vegetation in the middle of the pond. Charles W. Myers informed me that at Penonomé, Coclé, Panamá, he found *staufferi* calling from grass in puddles where *microcephala* was absent, and at El Caño, Coclé, Panamá, *staufferi* was calling from higher sites ("several inches to a few feet above water") than *microcephala*.

Stuart (1948:34) reported breeding individuals from La Libertad, Guatemala, after rainfall in late May, and Schmidt and Stuart (1941:239) reported *staufferi* breeding in July in the Salamá basin, Alta Verapaz, Guatemala. Stuart (1935:38) and Duellman (1960:63 and 1963:226) agreed that this species breeds early in the rainy season. However, Rand (1957:519) stated that in El Salvador "these frogs did not begin to call until almost a month and a half after the beginning of the rains." Blair (1960:133) reported that males call in June and July in Chiapas, Oaxaca, Veracruz, and Tamaulipas, México.

The mating call of this species is a series of closely spaced notes having a fundamental frequency of about 100 cycles per second. Each note has a duration of 0.13 to 0.23 second, repeated at intervals that are longer than the duration of the call. The notes are moderately low-pitched and have a dominant frequency of more than 3,000 cycles per second and about 120 pulses per second (Table 2).

Tadpoles.—Measurements of the 33 tadpoles that are available are given in Table 8. The largest tadpole examined is in stage 38 and has a total length of 29.5 mm.

A typical tadpole in stage 38 of development (KU 104162, 5 km ESE Córdoba, Veracruz, México) has a body length of 10 mm., tail length of 19.5 mm., and a total length of 29.5 mm. Other characters are as follows: body as deep as wide, depressed anteriorly; body as long as depth of tail; interorbital space greater than distance between eye and snout but equal to internarial space; nostril equidistant between eye and tip of snout; distance between spiracle and eye less than distance between eye and snout; eyes large, situated dorsolaterally; mouth anteroventral, approximately triangular in outline; one row of papillae covering lower lip and all except median fourth of upper lip; scattered papillae at corners of mouth; tooth rows $\frac{2}{2}$; first upper row entire, second row interrupted medially, shorter than first; lower rows shorter than upper rows; beak weak; spiracle short and nearer eyes than anus; anal opening not reaching edge of ventral fin; dorsal fin barely extending onto body; caudal musculature pointed distally.

TABLE 8.—Sizes of Tadpoles of *Hyla s. staufferi* in Relation to Developmental Stages. (Means in parentheses below observed ranges; measurements in mm.)

Stage	N	Body length	Tail length	Total length
25.....	3	6.0-7.0 (6.7)	12.0-13.0 (12.5)	18.0-20.0 (19.2)
26.....	2	7.0-7.5 (7.3)	14.0-15.0 (14.5)	21.5-22.0 (21.8)
27.....	9	7.0-8.0 (7.6)	13.0-17.0 (14.5)	21.0-25.0 (22.0)
32.....	1	8.5	15.5	24.0
36.....	2	8.0-10.0 (9.0)	16.5-17.0 (16.8)	25.0-26.5 (25.8)
38.....	6	9.0-10.0 (9.6)	19.0-20.5 (19.5)	28.0-29.5 (29.1)
41.....	1	10.0	14.0	24.0
42.....	6	11.0-14.0 (11.8)	10.0-13.0 (11.9)	20.0-29.0 (24.8)
45.....	1	12.5	0.5	13.0
46.....	1	13.0

In life, body pale olive-tan, belly silvery white with pinkish-orange reticulations in some specimens; tail creamy white with silvery flecks and black or brown reticulations. In preservative, tan and pinkish-orange coloration lost; body transparent, reticulations on tail present.

Remarks.—*Hyla staufferi* was described by Cope (1865:195) on the basis of specimens from Orizaba, Veracruz, México. He described the color pattern as "color above dark olive, with a short black bar over each scapula, and one from eye to eye, with a trace along the coccyx." Cope (1887:14) placed *staufferi* as a subspecies of *Hyla eximia*, but he did not justify his action. Günther (1901:262) also considered *staufferi* to be conspecific with *eximia* without making any qualifying statement. Dunn and Emlen (1932:24) named *Hyla culex* from Tela, Honduras, on the basis of a male (MCZ 16098) having a snout-vent length of 25.1 mm., and a female (USNM 20267) from Patuca, Honduras. They diagnosed the species as having "discs larger than tympanum . . . black interorbital triangle, traces of black dorsal marking; three black bars on anterior and posterior face of thighs, two black bars on tibia, on tarsus and on forearm." The holotype now is faded but has some of the pattern described. Dunn and Emlen did not compare *culex* with *staufferi* but did compare it with *boulengeri* and *rubra*.

Dunn (1933:61) named *Hyla altae* from Summit, Canal Zone. His description was based on a male (MCZ 17972) having a snout-vent length of 25.1 mm., the color pattern was described as "gray with four darker dorsal stripes

. . . a faint trace of mid-dorsal striping. . . ." Dunn defined the the *Hyla rubra* group and recognized *boulengeri*, *altae*, *culex*, and *rubra* as members. *Hyla elaeochroa* and *staufferi* were omitted from his key to the group in Central America.

Kellogg (1932:174) compared *staufferi* with *eximia* and concluded that the two were probably distinct species. Stuart (1935:38) considered *altae* to be a synonym of *culex*. Gaige (1936:293) considered *altae* and *culex* to be conspecific but regarded *staufferi* as a different species. She also suggested that *staufferi* was not related to *eximia* but belonged to the *rubra* group. Taylor (1952:865) and Duellman (1966a:274) considered *altae* and *culex* to be synonyms of *staufferi*.

The only other worker besides Cope and Günther to consider *Hyla staufferi* as a member of the *eximia* group was Blair (1960:129), who suggested the relationship on the basis of similarities in the structure of the calls of *eximia* and *staufferi*. Taylor (1938:421) and Smith and Taylor (1948:78) excluded *staufferi* from the *eximia* group on the basis of morphological characteristics. I consider *culex* to be inseparable from *staufferi*, whereas *altae* is recognizable as a Panamanian subspecies of *staufferi*.

Hyla staufferi staufferi Cope, New Combination

Hyla staufferi Cope, Proc. Acad. Nat. Sci. Philadelphia, 17:195, October 1865 [Holotype.—USNM 15317, Orizaba, Veracruz, México; Francis Sumichrast collector]. Brocchi, Mission Scientifique au Mexique et dans L'Amerique Centrale, 1881, p. 36. Boulenger, Catalogue, of the Bratrachia Salientia s. Ecaudata, p. 400, February 1, 1882. Kellogg, Bull. U. S. Natl. Mus., 160:173, March 31, 1932. Smith and Taylor, Bull. U. S. Natl. Mus., 194:88, 1948. Taylor, Univ. Kansas Sci. Bull., 35:862, July 1, 1952. Rand, Fieldiana Zool. Chicago Nat. Hist. Mus., 34:518, April 18, 1957. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 17:274, June 17, 1966.

Hyla eximia staufferi Cope, Bull. U. S. Natl. Mus., 32:14, January 16, 1887.

Hyla eximia (part): Günther, Biologia Centrali-Americana, Reptilia and Batrachia, p. 261, June 1901. Nieden, Das Tierreich, Anura I, p. 245, June 1923.

Hyla culex Dunn and Emlen, Proc. Acad. Nat. Sci. Philadelphia, 84:24, March 22, 1932 [Holotype.—MCZ 16098, Tela Honduras; Raymond A. Stadelman collector]. Stuart, Misc. Publ., Univ. Michigan Mus. Zool., 29:38, October 1935. Gaige, Carnegie Inst. Washington Publ., 457:293, 1936.

Diagnosis.—Small frogs (♂ to 29 mm., ♀ to 31.6 mm.); dorsolateral stripes irregular; paravertebral stripes usually broken; two or three transverse bars on shanks; thighs spotted or not; arms usually barred; interorbital bar usually present; toes about three fourths webbed; color brown, tan, or olive-green.

Variation.—Three hundred and sixty males chosen at random from throughout the range have snout-vent lengths of 20.7 to 29 mm. (25.9 mm.). The smallest individuals are from Costa Rica and Nicaragua (means 24.2 and 24.4 mm., respectively). The largest individuals are from Guatemala and El Salvador (mean of each 27.0 mm.). The ratio of the diameter of the tympanum to that of the eye is more than 60 per cent in most samples, but in those from Costa Rica and British Honduras it is smaller. The color pattern is highly variable. Some specimens are dark brown or pale brown in color. Incomplete dorsal stripes are present in 94.6 per cent of the specimens, and transverse bars are present on the shanks in 98.3 per cent of the specimens. The inter-

orbital spot varies from transverse to longitudinal in position, and an irregular white line extends from the upper jaw to the arm in some specimens (Table 7).

Distribution.—*Hyla staufferi staufferi* inhabits savanna and subhumid and xeric forests in the lowlands and moderate elevations from southern Tamaulipas southward to Nicaragua on the Caribbean versant and from Guerrero, México to northwestern Costa Rica on the Pacific lowlands (Fig. 7). Duellman (1963: 226) commented that a specimen from Chinajá, Guatemala, possibly was transported there in the cargo from Toocog, because with this one exception the species is unknown in tropical rainforest in Guatemala.

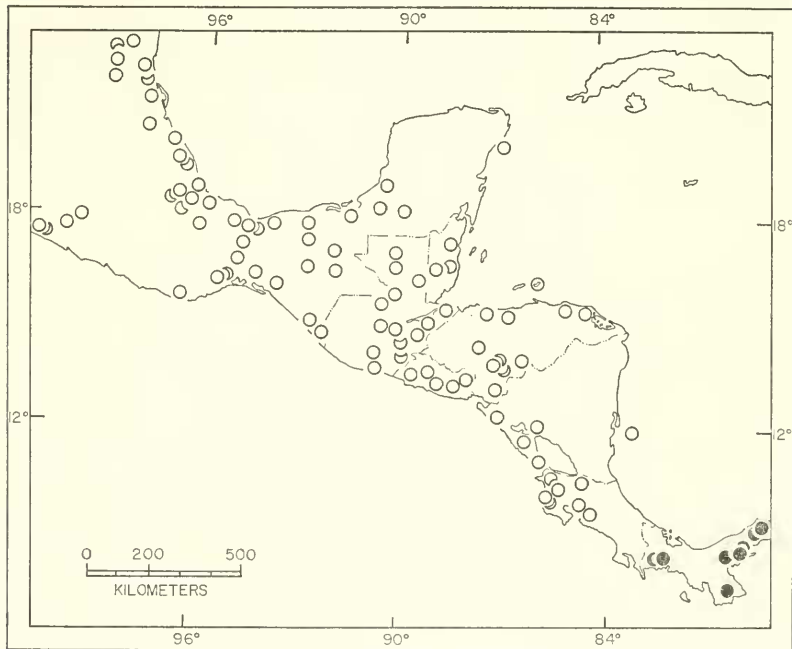


Fig. 7. Map showing locality records for *Hyla staufferi staufferi* (circles) and *H. staufferi altae* (dots).

Specimens Examined.—México: *Campeche*: 5 km S Champotón KU 71296-7; 7 km W Escárcega, KU 71298-308; 13 km W, 1 km N Escárcega, KU 71309-10, 75090-4. *Chiapas*: 32 km S Arriaga, KU 57789-92; 4 km N Ixtapa, KU 5776-81; 3.6 km SW Las Cruces, KU 37740; 17 km S Las Cruces, KU 57793-4; 24 km S Las Cruces, KU 104160 (tadpoles); 11 km S Tapachula, KU 57782-8, 60000 (young). *Guerrero*: El Limoncito, near La Venta, KU 31392-401; Mexcala, near Balsa River, KU 31391; Organos, S El Trienta, KU 31390. *Oaxaca*: 26 km N Matías Romero, KU 33878-82; 2.5 km S Pochutla, KU 59924-7 (skeletons); 5 km S Pochutla, KU 57795-801; 3.2 km E Tapanatepec, KU 37877-902; 17.6 km WNW Tapanatepec, KU 65033-4; Temascal, USC 8243 (8); 3.2 km S Toluca, KU 39657-8; 0.5 km Tuxtepec, KU 87073-81, 87610 (tadpoles); 17 km S Tuxtepec, KU 65035-7; 1 km W Zanatepec, KU 104161 (tadpoles). *Quintana Roo*: Isla Cozumel, 3.5 km N San Miguel, KU 71710-11 (young). *San Luis Potosí*: Valles, KU 31490. *Tabasco*: Teapa,

UMMZ 118887 (3), 119203 (13); 9.6 km N Teapa, UMMZ 119202; 24 km N Teapa, UMMZ 119961 (5); 29 km N Teapa, UMMZ 119960; 3.5 km S Villahermosa, UMMZ 119201 (2); 17.6 km S Villahermosa, UMMZ 119200 (8). *Tamaulipas*: 1 km E Chamal, UMMZ 110706; Gómez Farías, UMMZ 110701 (3); 5 km SE Gómez Farías, UMMZ 110705; 8 km NE Gómez Farías, UMMZ 11282 (2), 11283 (3); Kilometer 615 between Río Limón and Llera, UMMZ 80455 (2); 5 km W San Geraldo, UMMZ 110702 (4), 110703 (3); 8 km W San Geraldo, near Río Frío, UMMZ 110704 (5). *Veracruz*: 3 km SW Boca del Río, KU 10494-8; 5 km SW Boca del Río, KU 23701; 5 km ESE Córdoba, KU 104162 (tadpoles); Cuautlapán, KU 57098-102, 26787; Hacienda Tamiahua, Cabo Rojo, KU 62871; 2 km ENE Mata Oscura, KU 105627; 5 km SE Paso del Toro, KU 40144; Portrero Viejo, KU 23911-2, 26786, 27413, 57094-7.

Guatemala: *Alta Verapaz*: Chinajá, KU 57769; Finca La Cubilquitz, UMMZ 90871, 90872 (5), 91379 (2). *Baja Verapaz*: 1 km S San Jerónimo, UMMZ 84077 (7), 84078 (14). *Chiquimula*: 1.6 km SE Chiquimula, UMMZ 98114 (2); Esquipulas, UMMZ 106784 (4), 106785 (14). *El Petén*: No specific locality, USNM 25143, 24825-6; La Libertad, FMNH 27096-7, KU 57770, UMMZ 75339 (15), 75340 (15), UMMZ 94341-2. *Esquintla*: 20 km N San José, AMNH 74369-76. *Guatemala*: 16 km NE Guatemala, KU 43539. Izábal: Puerto Barrios, TCWC 16671-73, 16646-56; 2.5 km NE Río Blanco, KU 57774-5. *Jalapa*: Jalapa, UMMZ 106788 (44). *Jutiapa*: Finca La Trinidad, UMMZ 107730 (12), 107731 (16); Jutiapa, UMMZ 106786 (2). *Zacapa*: 14 km ENE Mayuelas, KU 57773; 7 km ENE Río Hondo, KU 57771-2, 59999 (young).

British Honduras: *Belize*: Belize, FMNH 4406. *El Cayo*: San Agustín, UMMZ 80741 (8). *Stann Creek*: 10 km S Stann Creek on Hummingbird Highway, UMMZ 125720-1.

El Salvador: *Cuscatlán*: 7 km WNW Cojutepeque, TNHC 32004-10. *La Libertad*: 16 km NW Santa Tecla, KU 43540-1. *La Unión*: 2.5 km Santa Rosa, TCWC 16669-70. *Morazán*: Dividendero, USNM 73288-92. *San Salvador*: San Salvador, FMNH 65101-06, KU 61932-44, 61989-92, 62152 (eggs), USNM 117588, 118391 (3), 118394; 1.6 km NW San Salvador, KU 43162-3.

Honduras: *Atlantida*: Ceiba, USNM 117592. *Choluteca*: Choluteca, KU 85361-6; 2 km E Choluteca, UMMZ 118395 (7); 3.2 km NE Choluteca, KU 100500-01; 6.2 km E Choluteca, KU 65046-56; 10 km E Choluteca, KU 65045; 5 km S Choluteca, USC 2700 (4). *Colón*: Isla Guanaja (Islas de la Bahía), TCWC 21551, TNHC 32011. *Cortés*: Agua Azul, TCWC 19178-9; East side Lago Yojoa, KU 65038-44. *El Paraíso*: Valle de Jamastrán, AMNH 54800-04. *Francisco Morazán*: Escuela Agrícola Panamericana, AMNH 54963-73; 14.5 km NW Comayagüela, KU 100499; El Zamorano, KU 103224; 29 km N Tegucigalpa, TNHC 32003, 32012.

Nicaragua: *Chinandega*: Finca San Isidro, 10 km S Chinandega, KU 85311-33. *Managua*: 13 km E Managua, KU 85339; 2 km S Tipitapa, KU 85334-8. *Rivas*: 9.5 km SE Rivas, KU 85355-6; 18 km SE Rivas, KU 85354; 7.7 km NE San Juan del Sur, KU 85346-53; 16.5 km NE San Juan del Sur, KU 85340-5; 5 km SE San Pablo, KU 43151-61. *Zelaya*: Isla Grande del Maiz, KU 85357-60.

Costa Rica: *Alajuela*: *Los Chiles*, USC 7215 (2), 7217. *Guanacaste*: 4 km W Bagaces, USC 7019 (5); Finca Taboga, KU 102265-5; 12 km S La Cruz, USC 8091; Las Cañas, KU 41113 (skeleton); 27 km N Las Cañas, USC 8171 (5); Guardia, Río Tempisque, USC 8214; 10 km N Guardia, KU 102266-7; 1.6 km N Guayabo de Bagaces, USC 7023 (3); Liberia, KU 36510-22; 4 km W Liberia, KU 36449-64, USC 102 (10), 103 (9), 104 (7), 105; 6 km N Liberia, USC 8096; 8 km NNW Liberia, KU 65032; 14.5 km N Liberia, USC 8079, 8138 (2); 14.5 km S Liberia, USC 8238 (5); 6 km N Nicoya, USC 8229 (11); 4 km S Nicoya, USC 8230, 8231; Peñas Blancas, KU 102263; 8.6 km ESE Playa del Coco, USC 8137 (14); 21 km E Playa del Coco, USC 8138 (2); Santa Cruz,

USC 8232 (2); 3 km E Santa Rosa, TCWC 16663-68; Tenorio, KU 32159; Tilarán, KU 36509. *Puntarenas*: 10 km WNW Esparta, KU 65022-9, 68614 (skeleton); 4.5 km WNW Esparta, KU 65030; 12 km WNW Esparta, KU 65031; 6 km E Esparta, KU 86477; Hotel Maribella, KU 32157-8; 3 km W Puntarenas, TCWC 16657-62.

Hyla staufferi altae Dunn, New Combination

Hyla altae Dunn, Occas. Papers Boston Soc. Nat. Hist., 8:61, June 7, 1933 [Holotype.—MCZ 17972, Summit, Canal Zone, Panamá; Emmett R. Dunn collector].

Hyla culex: Stuart, Misc. Publ. Univ. Michigan Mus. Zool., 29:38, October 1, 1935. Gaige, Carnegie Inst. Washington Publ., 457:293, 1936.

Hyla staufferi: Taylor, Univ. Kansas Sci. Bull., 35:862, July 1, 1952. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 17:274, June 17, 1966.

Diagnosis.—Small frogs (δ to 26 mm., ♀ to 27 mm.); dorsolateral and paravertebral stripes complete; longitudinal dark gray stripe on shank; thighs unmarked; interorbital bar usually absent; toes about three fifths webbed; gray to brownish gray above.

Variation.—*Hyla staufferi altae* is less variable in size, proportions, and color pattern than is *H. s. staufferi*. The size varies from 21.7 to 26 mm. (23.6) in 72 males. The ratio of tibia to snout-vent length is 0.42 to 0.50 (0.45), slightly less than in the northern subspecies. In color pattern 94.5 per cent of the individuals have complete dorsal stripes, and all have a longitudinal stripe on the shank (Table 7).

Distribution.—This subspecies is restricted to subhumid forests and savannas on the Pacific lowlands of Panamá. *Hyla s. altae* is presently known to occur from Chepo in east-central Panamá through the Azuero Peninsula to Concepción, Chiriquí, in western Panamá (Fig. 7).

Specimens Examined.—Panamá: Canal Zone: No specific locality, TNHC 24406; 2.8 km SW Fort Kobbe, KU 101679. Chiriquí: 14.4 km E Concepción, AMNH 69799-801; 6.6 km N David, TNHC 32013-4; 2 km S David, AMNH 68802. Coclé: 1 km NE El Caño, KU 101662-75; El Valle de Antón, AMNH 59601-5, KU 77333-47; 7 km SSW Penonomé, KU 101654-61. Los Santos: Tonosí, KU 101246 (tadpoles), 101697-701. Panamá: 2 km WSW Chepo, KU 101680-8; 6 km WSW Chepo, KU 77324-27; El Cangrejo (Panamá), KU 101676-8; Nueva Gorgona, AMNH 69991, 69798; 1.5 km W Pacora, KU 77328-32; 2 km N Tocumen, KU 101689-95; 8 km NE Tocumen, KU 101696.

EVOLUTIONARY HISTORY

My assumptions regarding the evolutionary history of the *Hyla rubra* group in Central America were derived partly from interpretations of the evolutionary history of other animal groups (Simpson, 1943, 1965; Dunn, 1931b; Stuart, 1950; Duellman, 1958, 1960, 1963, 1965; and Duellman and Trueb, 1966). The origin and early evolution of the group probably occurred prior to the Mid-Pliocene in the lowlands of South America, because the greatest diversity of the group is in Brazil. Differentiation into two or more subgroups took place in South America prior to the late Pliocene. At the end of

the Pliocene, shortly after the closure of the Colombian Portal, many South American animals migrated into Central America (Simpson, 1943, Maldonado-Koerdell, 1964, and Savage, 1966). It is likely that the *Hyla rubra* group entered Central America at that time; apparently two stocks (*rubra-elaeochroa-staufferi* stock and *boulengeri-foliamorta* stock) migrated into Central America.

Hyla elaeochroa is closely related to *rubra* and probably differentiated from *rubra* through spatial isolation. Thus, we have *elaeochroa* in Central America and *rubra* in South America; most likely only in relatively recent times has *rubra* migrated into eastern Panamá from northern South America. The differentiation and dispersal of *elaeochroa* and *staufferi* took place in Central America after the Pliocene. Probably the events of the Pleistocene resulted in the isolation of populations. One of these (*Hyla staufferi* stock) was restricted in the subhumid Pacific lowlands, whereas the *Hyla elaeochroa* stock occupied the tropical wet forests of the Caribbean lowlands. *Hyla elaeochroa* apparently more closely resembled the parental stock by being restricted to the tropical rain forests, whereas *staufferi* adapted to subhumid environments and thereby was able to disperse throughout most of the subhumid regions of Central America.

After geographical separation took place the initial genetic divergence between the two populations was maintained by means of ecological and ethological isolating mechanisms. Under these circumstances it can be supposed that the different ecological preferences of *elaeochroa* and *staufferi* depend on the climatic changes that took place during the Pleistocene. On this basis it may be proposed that when the original prototype broke up into the two incipient species, the *staufferi* stock became physiologically and behaviorally adapted to subhumid conditions and dispersed into dry areas of the lowlands of Middle America. The tropical evergreen forests on the Caribbean side of lower Central America and the uplift of the Talamanca range in the Pliocene were barriers to the dispersal of *staufferi*. Consequently, this frog dispersed along the Pacific lowlands.

At the present time *staufferi* occupies the length of the Pacific lowlands in Central America, except in the rainforest of the Golfo Duce region, which apparently is a relict stand and now separates the ranges of two subspecies of *Hyla staufferi*. This species crossed the central Nicaraguan lowlands and reached the Caribbean lowlands of Nicaragua and nuclear Central America. The species